PHYLOGENETIC RELATIONSHIPS, SEED CHARACTERS, AND DISPERSAL SYSTEM EVOLUTION IN AMARYLLIDEAE (AMARYLLIDACEAE)[1]

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ABSTRACT

The phylogeny of the mostly African tribe Amaryllideae is presented as a basis for classification and an enquiry into the evolutionary interrelationship between seed and fruit characters and seed dispersal modes. The cladistic analysis is based on morphological, seed anatomical, and cytological data, of which seed and fruit specializations are illustrated. Three dispersal modes, anemochory, atelechory/rain wash, and autochory, are optimized onto the selected cladogram and the pattern is considered in terms of functional fruit and seed morphology. The new classification recognizes two monophyletic subtribes: Crininae (*Boophone* sensu stricto, *Crinum, Ammocharis,* and *Cybistetes*) and Amaryllidinae (*Amaryllis, Nerine, Brunsvigia, Crossyne, Hessea, Strumaria,* and *Carpolyza*). The phylogeny suggests that in Amaryllidinae the ability of the green, stomatose seeds to mature after they are released favored the development of rapidly shed, wind-tumbled infructescences in three clades especially in semiarid, southwestern Africa. In Crininae the seeds are large, cork-covered, endosperm-rich, and relatively slow developing. The limited seed dispersal mode in *Crinum* and *Ammocharis* appears to be a consequence of the derived indehiscent fruit, which is basal in Crininae, and the anchoring function of their persistent, lax scape.

Amaryllideae, a monophyletic group consisting of 11 currently recognized genera and approximately 155 species, is one of nine tribes (sensu Dahlgren et al., 1985) in the monocotyledonous family Amaryllidaceae. The members are all bulbous herbs with distichous or rarely rosulate leaves and a lateral, solid, naked scape which is terminated by an umbel-like cluster of flowers. Their seeds are characteristically large and nondormant. Although remarkably uniform in floral and vegetative morphology, much diversity exists in the tribe's fruiting structures, some of which function as specialized units of dispersal in wind or water. Members of the tribe inhabit grassland, savanna, and tropical forests in sub-Saharan Africa, but are most speciose in southern Africa, where habitats include semiarid, dwarf shrublands in a winter-rainfall climate. The tribe's only pantropical representative is *Crinum* L., which extends from Africa to Madagascar, the Mascarene and Pacific Islands, and the tropics of America, Asia, and Australia.

Several Amaryllideae have traditional and eco-nomic uses. The charred and crushed bulb scales of *Ammocharis coranica* (Ker Gawl.) Herb. have been used as an adhesive (Phillips, 1917, 1938), and a decoction of the bulbs of *Boophone* Herb., *Brunsvigia* Heist., *Crinum,* and *Nerine* Herb. have provided medicine and poison to many African people (Phillips, 1917; Watt & Breyer-Brandwijk, 1962). The use of the highly toxic bulbs of *Boophone disticha* (L.f.) Herb. for arrow poison by early hunter-gatherers has been particularly well documented (Bradlow, 1994; Forbes, 1986; Forbes & Rourke, 1980). Numerous forms and hybrids of *Nerine, Amaryllis* L., and *Crinum* are cultivated for their elegant flowers, and the spherical fruiting heads of *Boophone* and *Brunsvigia* are locally gathered for dried floral arrangements.

Amaryllideae were first delimited as monophyletic by Traub (1965, 1970), who recognized the presence of threadlike "fibres" in torn-off leaves and bulb scales as diagnostic for the tribe (character 1). This feature has since been corroborated by four non-homoplasious synapomorphies: uniteg-

Table 1. Major recent classifications of Amaryllideae.

	Crinum, Ammocharis, Cybistetes, Boophone	Amaryllis, Nerine, Brunsvigia	Hessea, Carpolyza, Strumaria	Crossyne
Traub (1957)	Crininae	Crininae	Strumariinae	
Traub (1962)	Crineae	Crineae	Hesseae	
Traub (1963)	Crineae	Crineae	Strumarieae	
Traub (1965, 1970)	Crineae	Crineae	Crineae	
Dahlgren et al. (1985)	Amaryllideae	Amaryllideae	Amaryllideae	
D. & U. Müller-Doblies (1985)	Crininae	Crininae	Strumariinae	
Snijman & Linder	Crininae	Amaryllidinae	Amaryllidinae	Amaryllidinae

mic ovules (Huber, 1969) and bisulculate pollen grains (Schulze, 1984) with spinulose exine sculpturing (Meerow, 1995), to which we add green embryos in nondormant, water-rich seeds (character 33).

Various subtribal classifications of Amaryllideae have been proposed (Table 1), most of which reflect the nomenclatural confusion introduced by Traub's (1957, 1962, 1963, 1965, 1970) continuous misapplication of the name Amaryllis to the unrelated genus Hippeastrum Herb. (Brummit, 1987). These systems differ only in the rank attributed to the two subtribal groups recognized in Amaryllideae (Crineae sensu Traub, 1965, 1970). Thus far, the relationships of the genera within these groups have never been disputed.

Amaryllidinae (Pax, 1887) or Crininae (Traub, 1957, 1963), the larger of the two subtribes, are characterized by the presence of minute "fibres" between the broken parts of leaves and bulb scales, a solid scape, and regular to zygomorphic flowers (Traub, 1963). Strumariinae, which are defined by no single character but by a combination of characters, comprise small plants with mostly two leaves surrounded by an amplexicaul cataphyll; regular flowers with a reduced perigone tube; filaments inserted into a sheath formed by the anther connective; and style variously connate to the filaments (Müller-Doblies, 1985).

Essentially these interpretations were limited to basic vegetative and floral morphological data and they were phenetically based; therefore the monophyly of the subtribal groups was never explicitly questioned.

The primary aim of this study was to use new morphological data from the infructescences, capsules, and seeds of Amaryllideae in a phylogenetic analysis to establish monophyletic groups of genera, and to assess the monophyly of the traditionally recognized subtribes Amaryllidinae and Strumariinae. Of special interest in Amaryllideae are the unique and complex seed dispersal mechanisms by

wind or water. To analyze the evolution of these dispersal mechanisms, changes in seed and fruit characters are traced on the phylogenetic tree to assess whether the different dispersal modes may have been facilitated by these functionally related characters. Lastly, in an attempt to establish evolutionary patterns in the ecology of Amaryllideae, we use the phylogeny to analyze the interrelationships between seed and fruit characters, dispersal traits, phenology, and phytogeography.

MATERIALS AND METHODS

CHARACTER ANALYSIS

Morphological data on Ammocharis Herb., Brunsvigia, Crinum, and Nerine were obtained from the literature, living collections at Kirstenbosch National Botanical Garden, and dried material at NBG. Crinum variabile (Jacq.) Herb. and all species of Amaryllis, Boophone, Crossyne Salisb., Carpolyza Salisb., Cybistetes Milne-Redh. & Schweick., Hessea Herb., and Strumaria Jacq. were studied in the field, and the South African summer-rainfall representatives of Crinum and Ammocharis were studied in cultivation.

Leaves, flowers, and seeds for anatomical study were fixed in FAA (90 ml 70% ethanol; 5 ml glacial acetic acid; 5 ml formaldehyde), subsequently dehydrated in an ethanol-toluene series, embedded in wax, and cut with a rotary microtome at 10–15 μm. Sections were stained with safranin and alcian blue, and photographed with a Zeiss Axioskop. Seeds examined by scanning electron microscopy were fixed in FAA, dehydrated in ethanol, and critical point dried before sputter-coating with Au/Pd. Photographs were taken with a Cambridge S200 SEM at 10 kV. Documentation for the taxa studied micromorphologically is given in Appendix I. The micromorphological characters reported here for C. variabile conform to published results of other African, Asian, and Australian species of the genus (Dutt, 1962, 1970; Howell & Prakash, 1990; Merry,

Table 2. Distribution of character states among the genera of Amaryllideae and subgenera of *Hessea* and *Strumaria*. Indeterminate states are coded as "?".

Haemantheae	00000	00000	00000	00000	00000	00000	0000
Crinum	10100	00100	?0000	11100	10011	10000	1110
Ammocharis	11100	00100	00000	11000	10011	10000	1110
Cybistetes	11100	00100	00000	11100	12011	10000	1110
Boophone	10000	00000	00000	11000	10111	00000	1110
Amaryllis	10000	00000	11000	11100	10000	00000	0010
Nerine	10000	00000	12000	11100	11000	00111	0010
Brunsvigia	11000	01010	12000	11100	12000	00111	0010
Crossyne	11001	01210	?2000	11100	12000	00111	0010
Hessea subg. *Hessea*	10010	00011	02002	11000	12000	00111	0010
Hessea subg. *Namaquanula*	10010	00011	01101	11000	12000	00111	0010
Hessea subg. *Kamiesbergia*	10010	00011	0201?	11000	12000	00111	0010
Strumaria subg. *Strumaria*	10000	00000	00000	11011	10000	00111	0011
Strumaria subg. *Tedingea*	100?0	00010	00000	11011	11000	00111	001?
Strumaria subg. *Gemmaria*	10010	100?0	00001	11011	12000	00111	0011
Carpolyza	10000	00010	00001	11001	11000	00111	0011

1937; Toilliez-Genoud, 1965; Venkateswarlu & Lakshmi, 1978). New seed data are provided for *Boophone, Ammocharis, Brunsvigia, Crossyne, Hessea,* and *Strumaria*.

Of the 34 morphological characters identified for the phylogenetic analysis, 5 have slightly overlapping states: leaf number, pedicel length, anther attachment, staminal tube length, and scape habit after seed set. The sets of different states recognized in these characters nevertheless proved to be informative, since the topology was considerably less resolved when they were excluded from the phylogenetic analyses. Only one of the four multistate characters was treated as unordered. Autapomorphies were excluded from the cladistic analyses but were later inserted onto the cladograms. Character state distribution is provided in Table 2.

CLADISTIC ANALYSIS

Cladistic analyses were carried out using the implicit enumeration (ie*) option of Hennig86 (Farris, 1988), and the tree bisection reconnection (TBR) branch swapping of PAUP (Swofford, 1993). Trees were rooted by designating an outgroup (Nixon & Carpenter, 1993). Anderberg and Tehler (1990) suggested that for taxonomic studies only strict consensus trees, containing only components retrieved by each of the complete set of most parsimonious trees, should be used. This is a very conservative approach, as these consensus trees are substantially less informative than the most parsimonious trees on which they are based (Farris, 1983), and they reveal little about process, as in character state change (West & Faith, 1990). Carpenter (1988) therefore argues that one of the most parsimonious cladograms should be preferred over a consensus

tree as a phylogenetic hypothesis. To choose among the set of most parsimonious trees, we use the logic that adding to the potential homoplasy of a character which is already highly homoplasious should not be as significant as adding to the potential homoplasy of an otherwise non-homoplasious character. Consequently, we select those topologies from the set of most parsimonious trees that minimize the possible homoplasy of the least homoplasious characters. There are several approaches by which this logic can be implemented. Goloboff (1993) developed a method for simultaneously downweighting homoplasious characters and locating parsimonious trees, but this has been criticized by Turner (1995). Meacham (1994) proposed a method for calculating the character compatibilities in a data set, and weighting those characters that are maximally compatible. We used the successive approximations weighting scheme implemented in Hennig86 using the rescaled consistency index: the product of the character consistency index and the character retention index (Farris, 1969; Carpenter, 1988). Maximally homoplasious characters, if they occur in only two taxa, would have a consistency index (CI) of 0.5, a rescaled consistency index of 0, and a weight of 0. Minimally homoplasious characters, with CI = 1 and retention index (RI) = 1, would have a rescaled consistency index of 1 and a weight of 10. In extreme cases Goloboff (1991a, b) has questioned the validity of using the rescaled consistency index as a measure for deciding which most parsimonious cladogram is to be preferred. Despite these reservations, successive approximations weighting analysis is considered to have value when used with caution (Crisp & Weston, 1995). Our preferred most parsimonious tree was com-

pared with the majority rule tree and the strict consensus tree, and decay analysis (Bremer, 1988; Donoghue et al., 1992) was conducted to provide measures of strength for the phylogenetic hypothesis represented by the most parsimonious tree topology. To investigate alternative hypotheses of monophyly, the additional cost of grouping *Amaryllis* within the *Boophone* clade was determined using MacClade (Maddison & Maddison, 1987). Character distributions on cladograms were examined, and figures were generated using CLADOS (Nixon, 1992).

To analyze the number of times a particular dispersal mode evolved and to determine its interrelationship with fruit, seed, and phenology states in the lineage, the dispersal modes and phenological states were plotted on the terminal taxa of the cladogram and the most parsimonious interpretation of the character states at each inner node was obtained using Farris optimization (Farris, 1970; Mickevich, 1982). The states coded for seed dispersal are taken from Van der Pijl (1982): anemochory (wind dispersal), which is divided into anemogeochory (tumbling) and anemoballists (wind ballists); atelechory (limited dispersal); and autochory (dispersal by the plant itself), which is used here in the passive sense. For the analysis of plant phenology, the foliage leaves were coded as synanthous (the leafing period coincides with the flowering period) or hysteranthous (the leafing period is separated from the flowering period).

All known seed and fruit characteristics were included in the data matrix for phylogeny construction, but for the analysis of dispersal mode only the abscission of the infructescence (character 22) was used. Following Deleporte (1993), the primary coding of such a character may not necessarily introduce circularity into our interpretation of dispersal system evolution.

CHARACTER CODING

The weightings determined by the successive approximations character weighting routine are given in parentheses and autapomorphies are marked with an asterisk.

1. (10) *Bulb scales*: without extensible elements when pulled = 0, with numerous extensible elements when pulled = 1.

Although Traub (1965, 1970) stated that "fibres" appear when the bulb scales and leaves of Amaryllideae are torn apart, an unpublished report (P. Goldblatt, pers. comm.) that these highly extensible elements are long, spirally thickened tracheids is

shown to be correct. Before elongation the tracheids are ca. 325 μm long and at all stages the wall thickenings are characteristically lightly stained by safranin. When artificially stretched the cottony appearance of these elements is reliably diagnostic for the tribe.

2. (3) *Outermost bulb scales*: fleshy to parchment-like = 0, hard and brittle = 1.

In the outgroup and most representatives of Amaryllideae, the outer tunics form brown, softly fibrous coverings. Bulbs with extremely thick coverings, which become hard and brittle, are found in *Ammocharis, Cybistetes, Crossyne,* and the *Brunsvigia* species with prostrate leaves. Although the chemical substances in these thick, dark brown or tan-colored tunics are unknown, these secondarily thickened bulb tunics are coded as a single state.

3. (10) *Leaf habit*: annual = 0, lasting longer than a year = 1.

A strictly annual growth pattern, in which just one set of foliage leaves is produced and shed each year, is found in most members of Amaryllideae and the outgroup. In contrast, *Crinum* species may either be evergreen or, as in *Ammocharis* and *Cybistetes,* they may have mature foliage leaves that die back during seasonal drought then regrow at the end of the dormant period. As Troll (1954) showed in *Ammocharis coranica* (Ker Gawl.) Herb., regrowth of the mature leaves is due to a well-developed intercalary meristem, which results in the truncate leaf apices that characterize most species in these genera. This growth pattern is particularly remarkable in plants of *Cybistetes longifolia* from the arid Richtersveld, southwestern Africa, in which the leaf blades elongate and die back up to three times during a single year in response to alternating wet and dry sequences (Snijman & Williamson, 1994).

4. (3) *Leaf number*: at least four = 0, two = 1.

A reduced number of foliage leaves is found in all species of *Hessea* and *Strumaria* subg. *Gemmaria.* Most individuals in these taxa have two leaves per year, but, rarely, three leaves have been recorded (Snijman, 1994). Four or usually more foliage leaves per shoot occur in all other Amaryllideae and in most genera of Haemantheae and the family.

5. *Leaf pigmentation*: unmarked = 0, speckled with red abaxially = 1.

Only in *Crossyne* are the leaves abaxially speckled with red, an autapomorphy for the genus.

6. *Leaf surface*: glabrous = 0, pubescent (at least in juveniles) = 1.

Leaves with soft, simple, uniseriate hairs (0.2–6.0 mm long) are unique to *Strumaria* subg. *Gemmaria*. Pubescence diminishes in some species of this group at maturity (*Strumaria* sect. *Bokkeveldia*) but is always present in juveniles. This specialization is treated as an autapomorphy.

7. (10) *Leaf margin*: unthickened = 0, heavily thickened = 1.

The leaf margins of *Brunsvigia* and *Crossyne* are raised with thick-walled cells, often giving the leaves a slightly crisped, reddened outline.

8. (10) *Leaf margin*: untoothed = 0, with thin-walled branching teeth = 1, with thick-walled branching bristles = 2.

Multiseriate, branching, cartilagenous cilia are present on leaf margins of *Crinum* (Arroyo & Cutler, 1984), *Ammocharis*, and *Cybistetes*, and these are thin-walled in comparison to the long, bristly cilia on the leaf margins of *Crossyne*. This multistate character is treated as unordered.

9. (4) *Pedicel length at anthesis*: equaling or less than perigone length = 0, at least twice the perigone length = 1.

Two variables determine inflorescence form at anthesis: pedicel length and flower size. A clustered inflorescence in which pedicel length is less than the perigone length predominates in Amaryllidaceae, but widely spreading inflorescences, with pedicels at least twice as long as the perigone, are characteristic of *Brunsvigia*, *Crossyne*, *Hessea*, and *Strumaria* subg. *Tedingea*. The states slightly overlap in *Nerine* and *Carpolyza*, but when partitioned according to the method of Almeida and Bisby (1984), the data for these taxa could be reliably scored (Snijman, 1992).

10. (10) *Flower color during senescence*: pigmentation accentuated = 0, pigmentation lost = 1.

Verdoorn (1973) first drew attention to color changes in the flowers of Amaryllideae when she noted that floral pigmentation in most southern African *Crinum* species is accentuated with age, whereas in a few species it is lost. Enhanced coloring is common in the senescent flowers of all genera of Amaryllideae and Haemantheae, except in *Hessea*, where pigmentation is consistently lost in all species. *Crossyne*, whose two species have contrasting states, was treated as indeterminate, and *Crinum* was scored as plesiomorphic until additional data clarify the interpretation.

11. (2) *Stamen position*: spreading = 0, declinate = 1.

Declinate stamens, absent from the outgroup, are consistently found in *Amaryllis*, *Nerine*, and *Brunsvigia*. Both states occur in *Crinum* and *Crossyne*, which are treated as indeterminate.

12. (4) *Staminal tube*: absent = 0, rudimentary = 1, conspicuous = 2.

Stamens in Amaryllideae are either separate (*Ammocharis*, *Boophone*, *Crinum*, and *Cybistetes*) or proximally connate to varying degrees. The connation in *Amaryllis*, coded as rudimentary, is extremely short (ca. 1 mm) and extends above the confluence of only the outer tepal whorl before becoming free. In *Nerine*, *Brunsvigia*, *Crossyne*, and *Hessea*, the staminal tube extends shortly to well above the confluence of both inner and outer tepal whorls, and is thus coded as conspicuous. Representatives of *Hessea* subg. *Hessea* may have the longest staminal tubes in the tribe, up to 4 mm long, in contrast to those of *Hessea* subg. *Namaquanula*, in which the tube is almost absent, putatively a secondary reduction (Snijman, 1994).

The interpretation of the stamens in *Strumaria* subg. *Strumaria* is more complex. Although separate in *S. bidentata* Schinz, the stamens in the remaining four taxa are connate. Serial sections in *S. truncata*, however, indicate that the outer stamens are proximally adnate to the style (Snijman, 1994). Thus the staminal connation in *Strumaria* subg. *Strumaria* is regarded as autapomorphic and treated independently from the staminal tube in other genera of Amaryllideae.

13. *Filament trichomes*: trichomes absent = 0, trichomes present = 1.

The filaments are smooth in all Amaryllideae and Haemantheae, except *Hessea* subg. *Namaquanula*, where they are proximally covered with short trichomes on the adaxial surface (Snijman, 1994).

14. *Filament morphology*: both whorls uniform = 0, outer and inner whorls dimorphic = 1.

Unknown elsewhere in Amaryllidaceae are the specialized, dimorphic filaments of *Hessea stenosiphon* (Snijman) D. & U. Müll.-Doblies. The short outer filaments occlude the perigone throat, whereas the inner filaments of this species are erect and club-shaped, with a structural composition highly representative of osmophores as described by Vogel (1990). The epidermal cells are densely cytoplasmic and the inner parenchyma contains strikingly conspicuous masses of starch (Snijman, 1994). Fra-

grance emission from these structures is still to be tested.

15. (4) *Anther attachment*: ± dorsifixed = 0, in a short connective sheath (subcentrifixed) = 1, in a long connective sheath (centrifixed) = 2.

Previously described as "basifixed" (Baker, 1888, 1896; Dyer, 1976; Phillips, 1951; Traub, 1963), the anthers of *Hessea* and *Carpolyza* were recently redefined in terms of the degree to which the filament tip is inserted into a tube formed by the anther connective. The relative lengths of the dorsal and ventral walls of the tubular connective enabled D. and U. Müller-Doblies (1985) to recognize three states of anther attachment: dorsifixed anthers (relative lengths less than 50%), subcentrifixed anthers (relative lengths 50–75%), and centrifixed anthers (relative lengths more than 75%). Despite their apparent arbitrary subdivision, current data indicate that the states are only slightly overlapping. Anthers are dorsifixed in the outgroup and in most genera of Amaryllideae; subcentrifixed in *Hessea* subg. *Namaquanula*, *Strumaria* subg. *Gemmaria*, and *Carpolyza*; and centrifixed in *Hessea* subg. *Hessea*. The interpretation of the anther attachment in *Hessea* subg. *Kamiesbergia* is not yet resolved (Müller-Doblies, 1992; Snijman, 1994). To reflect the hypothesized morphocline in anther attachment, the character states are treated as additive.

16. (10) *Pollen morphology* : monosulcate = 0, bisulculate = 1.

Relative to the large, boat-shaped-elliptic, monosulcate pollen grains in other genera of Amaryllidaceae (Meerow, 1995), pollen grains of Amaryllideae are consistently bisulculate and normally dispersed at the two-celled stage (Dutt, 1962; Erdtman, 1966; Howell & Prakash, 1990; Schulze, 1984).

17. (10) *Pollen exine*: reticulate = 0, spinulose = 1.

Unlike reticulate exine elsewhere in Amaryllidaceae, surface ornamentation of pollen is uniform in Amaryllideae; gemmate with scattered large spinulae (Meerow, 1995).

18. (1) *Style position*: symmetrically placed = 0, laterally displaced = 1.

The style is uniformly symmetrically placed in the outgroup, *Boophone*, *Ammocharis*, *Hessea*, *Strumaria*, and *Carpolyza*. All remaining Amaryllideae have a laterally displaced style. Lateral displacement of the style is usually associated with declinate stamens but in certain species of *Crinum*,

Crossyne, and *Cybistetes* the stamens remain evenly spread.

19. (10) *Style form*: slender = 0, proximally enlarged = 1.

With the exception of *Strumaria*, the style in Amaryllideae and the outgroup is typically slender. Goldblatt (1976) first recognized the proximally enlarged style in *Strumaria* as a derived, unique character. The stylar swellings are variable but take three basic forms: increasingly thickened upward then abruptly narrowed above (*Strumaria* subg. *Tedingea*); more or less equally thickened in the lower half (subg. *Strumaria*); or distinctly broadest at the base and gradually tapering upward (subg. *Gemmaria*) (Snijman, 1994).

20. (10) *Nectar collection site*: pooled around the style base = 0, in three discrete sites in the axils between the inner filaments and style = 1.

Nectar collects in a central well around the base of the style in the outgroup and in most genera of Amaryllideae. This contrasts with *Carpolyza* and *Strumaria*, where nectar collects in three discrete sites, in the axils between the inner filaments and the style base. These separate nectar collection sites vary in depth and diameter. In most species (*Carpolyza*, *Strumaria* subg. *Tedingea* and subg. *Gemmaria*), the site is shallow, holding nectar in a single large droplet. Through lengthwise and radial extension of the confluence formed by the outer filament whorl and style in *Strumaria* subg. *Strumaria*, the volume of the cavities between the inner filaments and style has been increased, and deep nectar wells have developed. Preliminary studies have shown that within *Strumaria*, nectary anatomy is quite diverse. Without exception the nectaries are septal, but considerable variation is found in the position of the nectaries relative to the locules, in their size, and their degree of convolution. Although the extent of septal nectary diversity in Amaryllideae does not approach that reported in Haemodoraceae (Simpson, 1993), a detailed study of floral anatomy may give further insight into the tribe's functional floral morphology.

21. (10) *Ovule*: bitegmic = 0, unitegmic = 1.

In contrast to the bitegmic ovules of most Amaryllidaceae, the ovules in Amaryllideae are unitegmic. Representatives reported to have a solitary integument are *Amaryllis* (Markötter, 1936; Oganezova, 1990; Schlimbach, 1924); *Boophone disticha* (Schlimbach, 1924); *Brunsvigia minor* Lindl. and several *Crinum* species (Hofmeister, 1861); *Cybistetes* (Markötter, 1936); and *Nerine sar-*

niensis (L.) Herb. (= *N. curvifolia* Herb.) (Goebel, 1932).

Furthermore, several species of *Crinum* have been described as having ategmic ovules (Toilliez-Genoud, 1965; Tomita, 1931). However, the definitive embryological studies of Dutt (1957a, b, 1959, 1962) and Venkateswarlu and Lakshmi (1978), on a range of *Crinum* species, present strong evidence for the existence of an integument before its loss during the transformation of the ovule into the seed. The present study also confirms the presence of unitegmic ovules in *Brunsvigia* and *Nerine* (see Appendix I) and reports their presence in *Crossyne*, *Hessea*, and *Strumaria*. This current data give further support to Huber's (1969) hypothesis that unitegmic ovules are synapomorphic for the tribe.

22. (1) *Scape habit during seed dispersal*: withering back after seed release = 0, detaching at ground level after seed release from the capsules = 1, detaching at ground level before seed release from the capsule = 2. 23. *Habit of fruiting cluster during seed dispersal*: remaining attached to scape = 0, detaching from scape = 1.

At maturity the scape in Amaryllideae varies in its duration and place of abscission. The scape persists above ground until long after seed release, then slowly withers away in the outgroup, *Amaryllis*, *Ammocharis*, *Boophone*, *Crinum*, and *Strumaria* subg. *Strumaria*. Elsewhere in the tribe, the scape detaches from the bulb at ground level soon after seed release (*Carpolyza*, *Nerine*, and *Strumaria* subg. *Tedingea*) or before the release of seed from the capsules (*Cybistetes*, *Brunsvigia*, *Crossyne*, *Hessea*, and *Strumaria* subg. *Gemmaria*). Thus through early abscission of the scape in the latter five taxa, the entire infructescence becomes the main unit of dispersal. Dispersal is similar in *Boophone*, but the structural unit is uniquely derived by the abscission of the entire fruiting cluster from the top of the scape. Multistate character 22 is treated as ordered, and until the abscission tissues of the scape are studied anatomically, the states are considered to be homologous.

24. (10) *Fruit*: dehiscent = 0, indehiscent = 1.

In the outgroup indehiscent fruits occur in four genera, whereas a dehiscent capsule is found only in *Cyrtanthus* L.f. Dehiscent capsules also occur uniformly in the closely similar Hippeastreae and Lycorideae (Dahlgren et al., 1985) and in Alliaceae, which molecular data identified as basal to Amaryllidaceae (Fay et al., 1994). Although not common in the outgroup, the existence of dehiscent

capsules in one representative, as well as at a level immediately basal to the Amaryllidaceae, formed the basis for selecting capsule dehiscence as the outgroup character state. This coding parallels Dahlgren and Rasmussen's (1983) hypothesis that baccate fruits are secondarily derived from capsules in Amaryllidaceae.

25. (10) *Developing fruit*: never rostellate = 0, rostellate = 1.

Ammocharis, *Boophone*, *Crinum*, and *Cybistetes* have fruits which, while developing, are beaked with the persistent base of the perigone tube. The beak persists on the mature fruits only in *Crinum*, and its final length has proved to be diagnostically valuable in many species (Nordal & Wahlstrøm, 1980; Verdoorn, 1973). None of the other members of Amaryllideae or the outgroup has beaked fruits.

26. (10) *Mature fruit*: ± regular = 0, irregular = 1. 27. *Mature fruit*: not large = 0, conspicuously enlarged = 1.

The form of the fruit is more or less symmetrical in Amaryllideae except in *Ammocharis*, *Crinum*, and *Cybistetes*, where it is molded by the enclosed developing seeds. As the shape of the seeds is often extremely variable (Manasse, 1990; Snijman & Williamson, 1994; Toilliez-Genoud, 1965), the fruit also assumes an irregular form. Conspicuously large, obconical to rarely spindle-shaped capsules (reaching up to 60 mm long and 25 mm across in many species), with visible transverse veining, are autapomorphic for *Brunsvigia*.

28. (10) *Testa*: without stomata = 0, stomatose = 1.

Although not common in the outgroup Haemantheae, dry seeds, crusted with phytomelan, occur in one representative, *Cyrtanthus*; widely in other Amaryllidaceae; and consistently in Alliaceae, the family basal to Amaryllidaceae (Fay et al., 1994). In contrast, the mature seeds of Amaryllideae are water-rich and lack phytomelan in the coat. Schlimbach (1924) was the first to report stomata on the seed coat of *Nerine sarniensis* (= *N. curvifolia*), and Boyd (1932) later recorded them in *Carpolyza spiralis* (L'Hérit.) Salisb. A survey of the testa in this study has shown that stomata are also present on the seeds of additional representatives of *Nerine*, in *Brunsvigia*, *Crossyne*, *Hessea*, and *Strumaria* (Appendix I). The stomata are anomocytic (Fig. 5B–E), as is typical for Amaryllidaceae (Arroyo & Cutler, 1984; Dahlgren & Clifford, 1982), and the surrounding cells are covered by a sculptured cuticle (Fig. 5D, E), in which the central striations become increasingly thick and sinuous with age.

29. (10) *Integument in developing seed*: disintegrating = 0, enlarging = 1. 30. (10) *Integument in developing and mature seed*: without chlorophyll = 0, chlorophyllous = 1.

In *Brunsvigia, Crossyne, Nerine, Hessea, Strumaria,* and *Carpolyza* the integument expands into a water-rich, chlorophyllous tissue with vascular strands. As reported in *N. sarniensis* (= *N. curvifolia*) this is achieved by increasing the number and the size of the cells after fertilization (Schlimbach, 1924), and when finally ripe, the integument contains rich amounts of starch and chlorophyll (Goebel, 1932) (Fig. 4B–D). In the other representatives of Amaryllideae the integument remains undifferentiated and finally disintegrates (Dutt, 1970; Venkateswarlu & Lakshmi, 1978), whereas in the outgroup, the integuments of seeds shed in a dry, dormant state are crushed at maturity.

31. (10) *Endosperm in mature seed*: undifferentiated externally = 0, formed into cork externally = 1. 32. (10) *Mature seed*: without chlorophyll in endosperm = 0, endosperm with chlorophyll = 1.

A novel feature in *Ammocharis, Boophone, Crinum,* and *Cybistetes* is the development of a few layers of cork tissue from the peripheral cells of the endosperm (Fig. 4E, F). Although well known in *Crinum* (Merry, 1937; Schlimbach, 1924; Venkateswarlu & Lakshmi, 1978) and *Cybistetes* (= *Ammocharis falcata* sensu Markötter, 1936), a cork-covered endosperm is reported here in two additional genera: *Boophone* and *Ammocharis* (Fig. 5F, H). Another novel feature in these genera is that chloroplasts occur in the peripheral cell layers beneath the phellogen, even when the seed is covered by the pericarp (Dutt, 1957a, 1962; Schlimbach, 1924). *Amaryllis* is the only taxon of Amaryllideae in which the extensively developed endosperm does not have corky or chlorophyllous outer layers (Schlimbach, 1924) (Fig. 4A). In all other Amaryllideae the endosperm remains undifferentiated and comparatively poorly developed.

33. (10) *Embryo*: without green pigment = 0, green = 1.

Dahlgren and Clifford (1982) suggested that the embryo of *Crinum* could be chlorophyllous. Since then Howell and Prakash (1990) recorded this feature in *Crinum flaccidum* Herbert, while our study confirms the presence of green-pigmented embryos in every genus in Amaryllideae. The chlorophyll content, however, is yet to be investigated.

34. (10) *Basic chromosome number*: 11 = 0, 10 = 1.

Chromosome numbers in Amaryllideae are well known (Goldblatt, 1972; Gouws, 1949; Nordal & Wahlstrøm, 1980) and a karyotype of $x = 11$ is considered basic in Amaryllideae (Goldblatt, 1976) and the family (Inariyama, 1937; Meerow, 1984; Satô, 1938). Species of *Carpolyza* and *Strumaria* have a reduced base number of $x = 10$ (Goldblatt, 1976; Snijman, 1994), the only exception being *S. pygmaea* Snijman, which has $x = 11$. Although most taxa in Haemantheae have $x = 9$ and 8 (Inariyama, 1937; Ising, 1970; Vosa & Marchi, 1980) some species of *Clivia* have the base number of $x = 11$ (Gouws, 1949).

OUTGROUP SELECTION

Traub's (1962, 1963) tribal classification of Amaryllidaceae provides a valuable framework for selecting an outgroup that has synapomorphies shared with the ingroup (see Nixon & Carpenter, 1993). Traub's system divides the currently recognized tribes (Dahlgren et al., 1985) into two infrafamily groups, the Amarylloidinae and the Pancratioidinae. Within the Amarylloidinae, the apparent close similarity between representatives of Amaryllideae and Hippeastreae (Brummit, 1987) is based essentially on highly homoplasious floral characters, but the pollen, fruit, and seed characters are discontinuous (see Meerow, 1995). Other differences between the two tribes are root and scape structure, and spathe valve arrangement, and in these characters Haemantheae is intermediate (Arroyo & Cutler, 1984). The close relationship postulated to exist between Haemantheae and Amaryllideae, for which equitant spathe valves (Arroyo, 1984) is a possible synapomorphy, thus accounts for our choice of Haemantheae as outgroup to root the cladogram. All the characters defined for the analysis of the Amaryllideae apply also to the outgroup Haemantheae.

DELIMITATION OF GENERA IN AMARYLLIDEAE

All the currently recognized genera of Amaryllideae were examined to ensure that their delimitation could reasonably be considered monophyletic. This is accomplished by identifying hypothetical synapomorphies of the ingroups relative to other taxa (Nixon & Carpenter, 1993). *Amaryllis, Carpolyza,* and *Cybistetes* were accepted as monophyletic by virtue of their being monotypic.

Boophone sensu lato (five species) has commonly been distinguished from other genera of Amaryllideae by large bulbs, inflorescences of more than 100 flowers, a perigone with tube shorter than the tepals, long pedicels in fruit, and triquetrous dry

fruits with solitary or few seeds per locule (Dyer, 1976; Nordal, 1982). Milne-Redhead and Schweickerdt (1939) first questioned the inclusion of species with both dehiscent and indehiscent fruits in *Boophone* and recommended that the generic limits be reexamined. In agreement with Müller-Doblies (1994), three groupings have been proposed for the five species.

(1) *Boophone disticha* and *Boophone haemanthoides* F. M. Leight. share indehiscent, beaked fruits, which are also found in *Crinum*, *Ammocharis*, and *Cybistetes*. However, the species are uniquely characterized by the abscission of the fruiting head from the top of the scape. Consequently, this species pair, which includes the type species of *Boophone*, is considered to be monophyletic. (2) *Boophone guttata* (L.) Herb. and *Boophone flava* W. F. Barker ex Snijman have leaves abaxially speckled with red, and fringed with long, rigid, branching hairs. These two unique features are taken as evidence of the monophyly of the species pair, and they are assigned to the genus *Crossyne*, which was recently resurrected by D. and U. Müller-Doblies (1994). (3) *Boophone pulchra* W. F. Barker shares none of the putative synapomorphies recognized for the newly defined *Boophone* and *Crossyne*. Possible derived characters in *Boophone pulchra*, relative to the tribe as a whole, include the presence of macropapillae on the adaxial leaf epidermis and enlarged, usually triquetrous capsules, features that occur in species of *Brunsvigia*. For the phylogenetic analysis of Amaryllideae, *Boophone pulchra* is, therefore, treated as belonging to *Brunsvigia* in accordance with D. and U. Müller-Doblies (1994). The only feature in which *Brunsvigia pulchra* (W. F. Barker) D. & U. Müll.-Doblies differs from other *Brunsvigia* species is the elongation of the pedicels after anthesis rather than prior to anthesis. Although typical of *Boophone* sensu stricto, this character state occurs in several other members of the tribe (*Amaryllis* and *Cybistetes*) and cannot be recognized as autapomorphic for *Boophone* sensu stricto.

Crinum is currently regarded as the largest genus in the tribe with ca. 65 species (Fangan & Nordal, 1993). Species concepts of these ornamental plants have traditionally been too narrow (Fangan & Nordal, 1993; Hannibal, 1985), and thus far revisional work for the African floras has resulted in a reduced number of taxa being upheld (Nordal, 1977). The genus is cytologically variable (Nordal & Wahlstrøm, 1980), but vegetative and floral diversity is comparable to that of other genera of Amaryllideae (*Brunsvigia*, *Hessea*, and *Strumaria*). Flowers vary from hypocrateriform to funnel-shaped or bell-shaped, with spreading or declinate stamens; the leaves, which sometimes form a false-stem, are channeled or ribbed, thin-textured or fleshy, with intact or truncate tips (Nordal, 1977). The truncate leaf apices, which also occur in *Ammocharis* and *Cybistetes*, result from a well-developed and putatively derived intercalary meristem (Troll, 1954), which enables the leaves to die back and regrow over several seasons. Evident synapomorphies do not exist to separate *Crinum* from *Ammocharis*; therefore, *Crinum* is probably paraphyletic with *Ammocharis* and *Cybistetes* embedded in it. However, for the analysis *Ammocharis* and *Cybistetes* are provisionally retained, as suggested by Snijman and Williamson (1994), and following the recommendations of Nordal (1977) and Verdoorn (1973) existing subgeneric divisions of *Crinum* are avoided because they are so weakly supported.

Nerine, with ca. 23 species, is possibly the second largest genus of Amaryllideae. Genera of Amaryllideae are distinguished by subtle floral characters, and the extremely similar floral morphology shared by species of *Nerine* provides good evidence for the proposed monophyly of the genus. The characteristic attenuate, more or less crisped, tepal outline of *Nerine* species is a likely synapomorphy for the genus.

Brunsvigia (19 species) is uniquely macropapillate on the adaxial leaf epidermis in many species (Arroyo & Cutler, 1984), and large, inflated capsules (sometimes up to 70 mm long) with visible transversal veins occur in all the species. Both features provide good evidence for the inclusion of *Boophone pulchra* in *Brunsvigia*. Although not inflated, similarly shaped, somewhat triquetrous or elongated dry fruits also exist in *Boophone* sensu stricto and *Cybistetes*. The different mode of dehiscence in the latter genera (indehiscent as opposed to dehiscent: character 24) suggests, however, that the fruits have been separately derived. The enlarged capsule is regarded here as evidence for the monophyly of *Brunsvigia*.

Hessea (13 species) and *Strumaria* (23 species), commonly distinguished by their consistently actinomorphic flowers, are the only genera of Amaryllideae currently classified to reflect explicitly established phylogenetic relationships. *Hessea*, with three subgenera, is defined by one unique synapomorphy: the total loss of floral pigmentation at senescence (Snijman, 1994). The synapomorphy for *Strumaria*, also with three subgenera, is the uniquely swollen or winged style base (Snijman, 1994). In order to provide maximum structure for the phylogeny of Amaryllideae, the reliably monophyletic subgenera of *Hessea* and *Strumaria* were
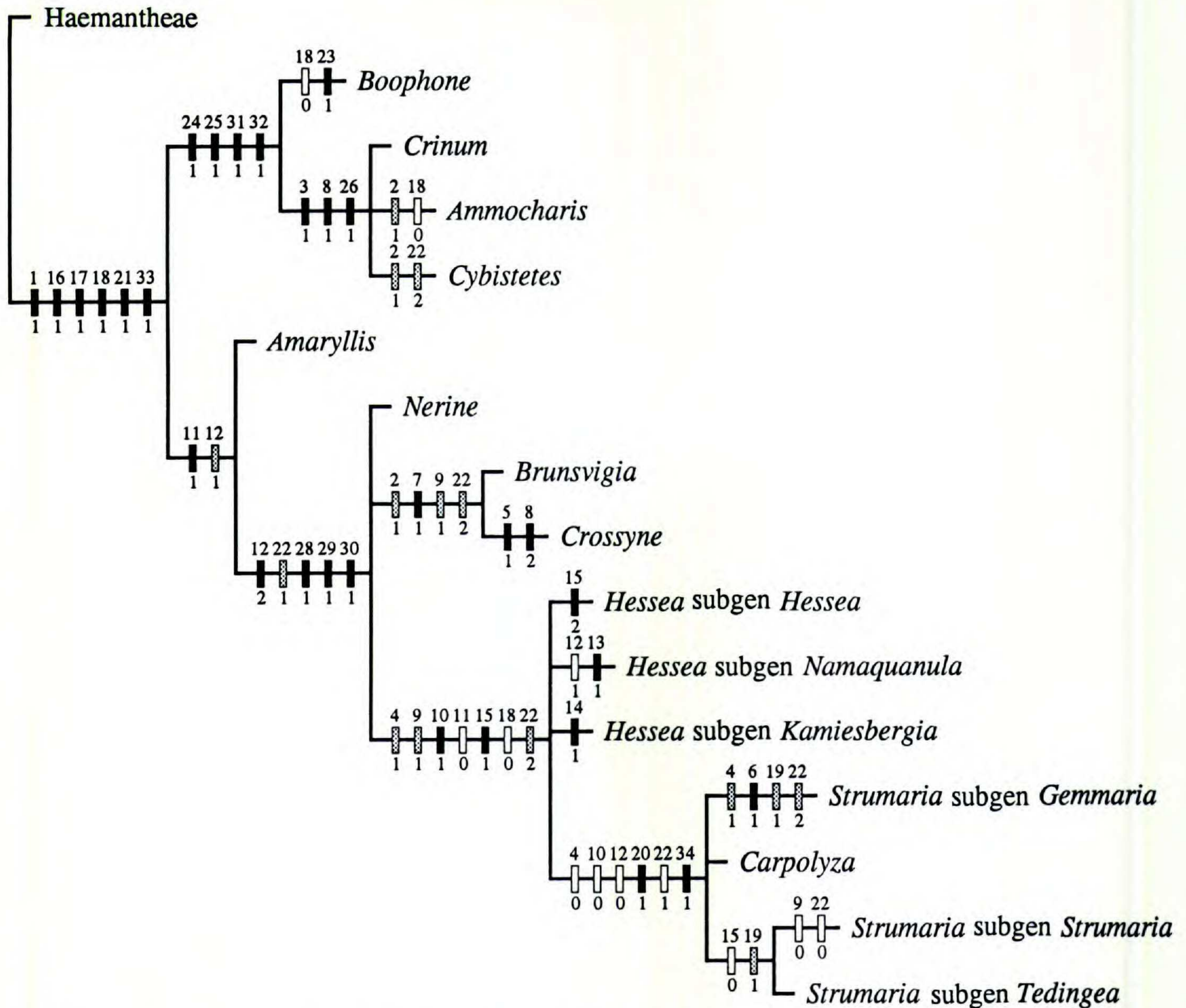
Figure 1. Strict consensus tree of Amaryllideae. Solid bars indicate non-homoplasious synapomorphies; gray bars indicate parallelisms and open bars indicate reversals.

also included in the analyses. All taxa included in the phylogenetic analyses are listed in Table 2.

RESULTS

The cladistic analyses with equal character weighting (excluding autapomorphies) gave 16 minimal length cladograms of 54 steps, a consistency index (CI) of 0.68, and a retention index (RI) of 0.80. The strict consensus tree (Fig. 1) generated by PAUP and Hennig86 shows that all 16 cladograms agree in the following respects. (1) *Boophone, Crinum, Ammocharis,* and *Cybistetes* appear as a monophyletic group. (2) *Amaryllis* resolves as basal to *Nerine, Brunsvigia, Crossyne, Hessea, Carpolyza,* and *Strumaria.* (3) *Brunsvigia* and *Crossyne* resolve in a monophyletic clade. (4) *Hessea, Carpolyza,* and *Strumaria* form a monophyletic group.

Successive weighting retrieved 2 of the 16 most parsimonious trees. These differ only in the degree of resolution shown in the *Hessea* clade. The tree

that we have chosen for interpreting character evolution (Fig. 2) differs from the strict consensus tree (Fig. 1) as follows. (1) The *Crinum–Ammocharis–Cybistetes* clade is more fully resolved. (2) *Brunsvigia, Crossyne, Hessea, Carpolyza,* and *Strumaria* form a clade that resolved in 14 of the 16 minimal length trees. (3) A clade of *Hessea* subgenera, which was retrieved in 10 of the 16 minimal length trees, is present. (4) The subgenera of *Strumaria* are present in a clade. Support for this component is more complex. *Strumaria* subg. *Gemmaria* is basal to *Carpolyza* and *Strumaria* subg. *Tedingea* and subgenus *Strumaria* in 10 of the minimal length trees, but this component is supported only by the homoplasious character 22(1) (CI 0.28, RI 0.54). In contrast, *Carpolyza* resolves as basal to the clade of *Strumaria* subgenera in 6 of the trees retrieved. However, character 19 (style proximally enlarged, CI 1.00 and RI 1.00), which supports the *Strumaria* clade, is unique in Amaryllidaceae (Snijman,
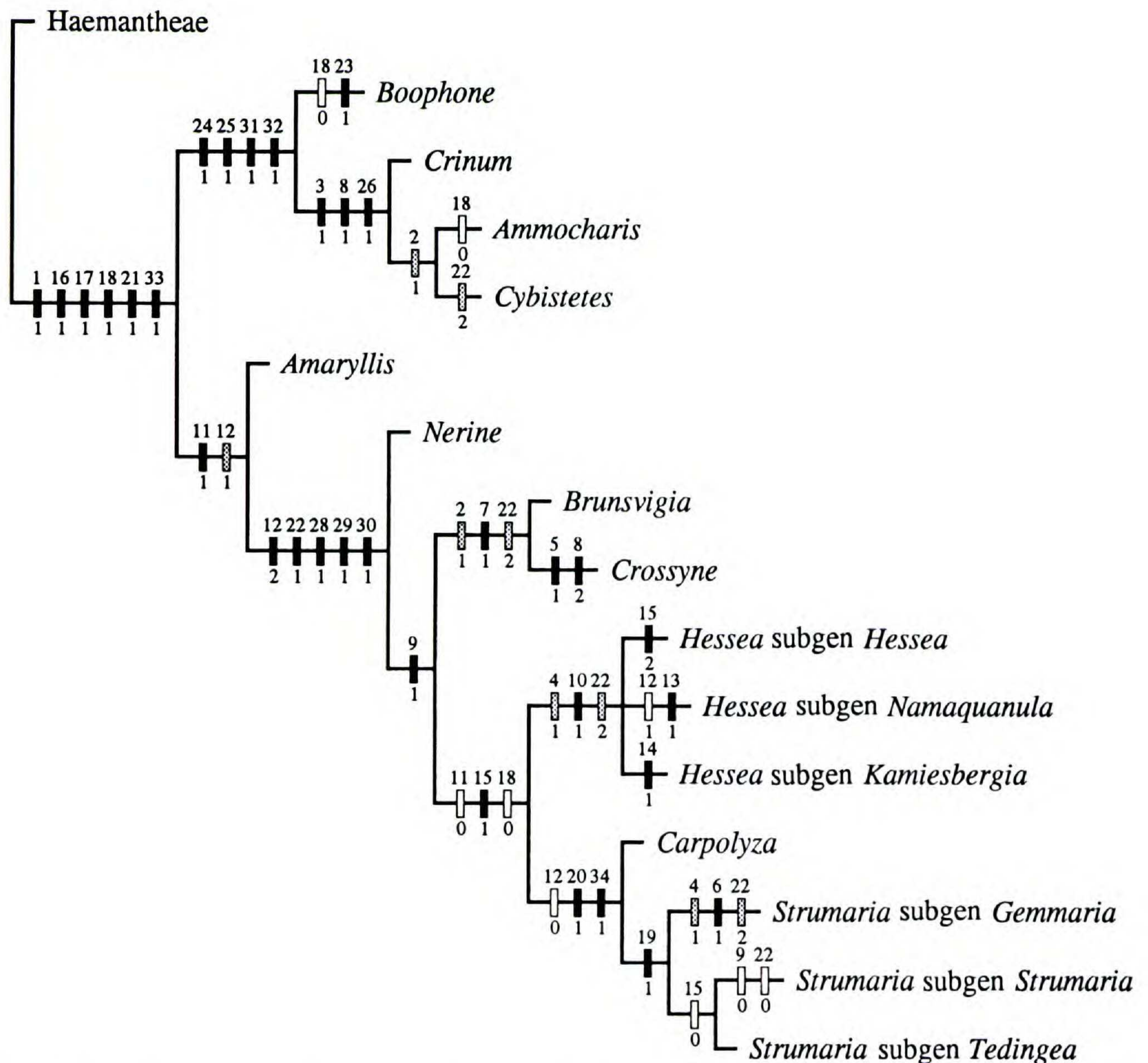
Figure 2. The preferred most parsimonious cladogram of Amaryllideae. Solid bars indicate non-homoplasious synapomorphies; gray bars indicate parallelisms and open bars indicate reversals.

1994), and we therefore accept the topology of the *Carpolyza–Strumaria* component in our preferred tree with confidence (Fig. 2). Lastly, the differences in resolution obtained in the *Crinum–Ammocharis–Cybistetes* clade in the strict consensus tree (Fig. 1) and the preferred most parsimonious tree (Fig. 2) do not alter our discussion of seed character and dispersal system evolution.

When *Amaryllis* was placed at the base of the *Boophone–Crinum–Ammocharis–Cybistetes* clade, as suggested by the classifications of Traub (1957, 1962, 1963), the topology was 2 steps longer than our most parsimonious tree. The placement of *Amaryllis* in a position basal to the two major clades gave a topology 1 step longer than the minimal length cladogram. When parsimony was relaxed by 2 steps, 1404 trees were generated and resolution was lost in all branches except the *Crinum–Ammocharis–Cybistetes* clade and the *Brunsvigia–Crossyne* clade.

DISCUSSION

RELATIONSHIPS WITHIN AMARYLLIDEAE

All previous classifications of Amaryllideae (Table 1) placed the *Boophone–Cybistetes* clade, *Amaryllis*, *Nerine*, and *Brunsvigia* in Amaryllidinae. Our cladistic analysis clearly shows that subtribe Amaryllidinae (=Crininae sensu Traub, 1957, 1963) is paraphyletic with *Crossyne* and Strumariinae (the *Hessea–Carpolyza–Strumaria* clade) embedded in it. Strumariinae, the only other subtribe previously recognized (Müller-Doblies, 1985), is monophyletic.

In order to recognize the monophyletic groups generated by the cladistic analysis we propose a new classification. It is widely accepted that nomenclature is most effective if taxon names are stable. Thus prior to translating cladistic results into new classifications, Linder (1991) recommends an assessment of the nodes that are unlikely to change

with the addition of new data. Since *Amaryllis* is the oldest valid name available for typification at subtribal level, the stability of its position is of particular importance. Our results best support the placement of *Amaryllis* basal to *Nerine, Brunsvigia, Crossyne, Hessea, Carpolyza,* and *Strumaria.* We have therefore chosen to join the Strumariinae clade with *Crossyne, Brunsvigia, Nerine,* and *Amaryllis* to form a more inclusive clade, which is formally named subtribe Amaryllidinae. The *Boophone, Crinum, Ammocharis,* and *Cybistetes* clade is accordingly recognized as a second subtribe: the emended Crininae. The option of recognizing a third subtribe, containing only *Amaryllis,* was also considered but we regard the formal classification given below to be more conservative in reflecting the presently understood relationship of *Amaryllis* to *Nerine* and other representatives of its clade. Nomenclatural stability within Amaryllideae is thus maintained until strong support to the contrary becomes available.

REVISED CLASSIFICATION OF THE TRIBE AMARYLLIDEAE

Tribe **Amaryllideae**

Bulb scales when torn produce extensible cottony threads; flowers actinomorphic or zygomorphic; pollen bisulculate; ovule unitegmic; seed water-rich with green embryo. Includes about 55 species. Mostly African but with several *Crinum* species in the tropics of Asia, Australia, and America, Madagascar, and the Mascarene and Pacific Islands.

Subtribe **Amaryllidinae** Pax in Engler & Prantl, Nat. Pflanzenfam. 2, 5: 105. 1887.

Scape usually abscissing at ground level; stamens declinate (except in *Hessea, Strumaria,* and *Carpolyza*), connate into a tube proximally (except in *Strumaria* and *Carpolyza*); seed (except in *Amaryllis*) with a well-developed chlorophyllous integument and stomatose testa. Includes 82 known species.

Amaryllis Linnaeus, Sp. Pl.: 292. 1753.

Flowers zygomorphic; stamens connate proximally into a rudimentary filament tube; seeds colorless or pink. Monotypic.

Nerine Herbert in Bot. Mag. 47: t. 2124. 1820.

Flowers zygomorphic; tepals attenuate, margins ± crisped. 23 species (Traub, 1967).

Brunsvigia Heister, Beschr. neu. Geschl.: 3. 1755.

Bulb scales usually thick and brittle; leaf mar-

gins raised; flowers zygomorphic; capsule enlarged, turbinate or fusiform with visible transverse veins; scape detaching at ground level; infructescence dispersed as a single unit. 19 species (Dyer, 1950, 1951).

Crossyne Salisbury, Gen. Pl.: 116. 1866.

Bulb scales thick and brittle; leaves speckled with red abaxially, margins raised and fringed with long, stiff trichomes; inflorescence 100- or more-flowered; flowers zygomorphic, sometimes only weakly so by deflexed style; scape detaching at ground level; infructescence dispersed as a single unit. 2 species (Müller-Doblies, 1994).

Hessea Herbert, Amaryllidaceae: 289. 1837.

Leaves usually 2; flowers actinomorphic, aging to brown; filaments inserted into a sheath formed by anther connective (centrifixed to subcentrifixed), except in *H. bruce-bayeri* (D. & U. Müll.-Doblies) Snijman and *H. stenosiphon* (Snijman) D. & U. Müll.-Doblies; infructescence dispersed as a single unit. 13 species (Snijman, 1994).

Strumaria Jacquin, Collectanea 5: 49. "1796" [1797].

Leaves up to 6, then usually arranged in a fan (subg. *Strumaria*), or mostly 2 and pubescent, at least in juveniles (subg. *Gemmaria*); flowers actinomorphic; filaments of outer or both whorls proximally adnate to style, usually inserted into a sheath formed by anther connective (subcentrifixed); style proximally swollen or winged; nectar collects in axils between inner filaments and style; basic chromosome number $x = 10$ (except in *S. pygmaea* Snijman, where $x = 11$). 23 species (Snijman, 1994).

Carpolyza Salisbury, Parad. Lond. 1: t. 63. 1807.

Flowers actinomorphic; inner filaments adnate to style proximally, inserted into a sheath formed by anther connective (subcentrifixed); nectar collects in axils between inner filaments and style; basic chromosome number $x = 10$. Monotypic (Snijman, 1994).

Subtribe **Crininae** Pax in Engler & Prantl, Nat. Pflanzenfam. 2, 5: 108. 1887.

Flowers actinomorphic or zygomorphic; fruit indehiscent, rostellate at least during development; seeds lacking an integument, endosperm-rich, cork-covered, with several layers of chlorophyll-containing cells below the phellogen. Includes ca. 73 species.

Table 3. Distributions and favored habitats of genera of Amaryllideae. Number of species is given in parentheses. Southern Africa is defined as the area south of a line between the Kunene and Zambezi rivers.

	Distribution	Habitat
Subtribe CRININAE		
Boophone (2)	Tropical East Africa to southern Africa	Open plains or slopes
Crinum (ca. 65)	Tropics of Africa, Asia, Australia & America, southern Africa, Madagascar, Mascarene & Pacific Islands	Moist sites, forests, river edges, seasonal pools or salt pans
Ammocharis (5)	Tropical East Africa to southern Africa	In rocks or seasonally wet places
Cybistetes (1)	Winter-rainfall region of southern Africa	Open sites
Subtribe AMARYLLIDINAE		
Amaryllis (1)	Winter-rainfall region of South Africa	Mesic places
Nerine (23)	Southern Africa	Mesic places
Brunsvigia (19)	Southern Africa	Open plains or rocky sites
Crossyne (2)	Winter-rainfall region of South Africa	Open places
Hessea (13)	Winter-rainfall region of southern Africa	In rocks and seasonally moist sites
Strumaria (23)	Winter-rainfall region of southern Africa	In rocks and seasonally moist sites
Carpolyza (1)	Winter-rainfall region of South Africa	In rocks and seasonally moist places

Crinum Linnaeus, Sp. Pl.: 291. 1753.

Leaves perennial, often formed into a false-stem, fringed with cartilaginous teeth, apex often truncate; flowers zygomorphic, sometimes only weakly so; fruit irregular, wall membranous to spongy. The genus has not yet been revised over its entire distribution range, but good regional treatments are available for Africa (Nordal, 1977, 1982; Nordal & Wahlstrøm, 1980; Verdoorn, 1973). Includes ca. 65 species (Fangan & Nordal, 1993) with ca. 40 in Africa. The genus is probably paraphyletic.

Ammocharis Herbert, Appendix: 17. 1821.

Leaves perennial; somewhat falcate, fringed with cartilaginous teeth, apex often truncate; flowers actinomorphic; fruit with membranous walls, irregular. 5 species (Milne-Redhead & Schweickerdt, 1939).

Cybistetes Milne-Redhead & Schweickerdt in J. Linn. Soc., Bot. 52: 191. 1939.

Leaves perennial, fringed with cartilaginous teeth, apex of mature leaves truncate; flowers weakly zygomorphic; scape detaching at ground level; infructescence dispersed as a single unit. Monotypic. The genus is probably nested in *Ammocharis* (Snijman & Williamson, 1994).

Boophone Herbert, Appendix: 18. 1821.

Leaves erect, distichous; flowers actinomorphic; fruiting head detaching from top of scape, dispersing as a single unit. 2 species.

PHYTOGEOGRAPHY AND PHENOLOGY

A comparison of the present distribution patterns of subtribes Amaryllidinae and Crininae (Table 3) shows that Crininae is widespread in the tropical and temperate regions of sub-Saharan Africa (Fig. 3). One genus, *Crinum*, is pantropical, with ca. 40 of its ca. 65 species in Africa (Nordal, 1982). Approximately 20 *Crinum* species occur in southern Africa, but only one is known from the winter-rainfall region (Verdoorn, 1973). Only three other representatives of Crininae (*Boophone disticha*, *Boophone haemanthoides*, and *Cybistetes*) are known in the temperate winter-rainfall region of southern Africa, although one of these (*Boophone disticha*) also ranges widely into central Africa. In contrast, Amaryllidinae is confined to the temperate regions of southern Africa (Fig. 3). Most *Nerine* species are known from the summer-rainfall region. *Brunsvigia* ranges widely over both summer- and winter-rainfall regions, whereas all the remaining representatives (*Amaryllis*, *Crossyne*, *Hessea*, *Carpolyza*, and all but two *Strumaria* species) are restricted to the winter-rainfall region of southern Africa. Most representatives of Crininae flower and fruit in summer during the leafing period. This differs in Amaryllidinae, where some species are summer-flowering but most flower and fruit in autumn, after the vegetative phase of the previous winter, which offers a short growing period.

SEED CHARACTERS IN AMARYLLIDEAE

Throughout the tribe, the seeds are water-rich, nondormant, and have chlorophyllous embryos. As
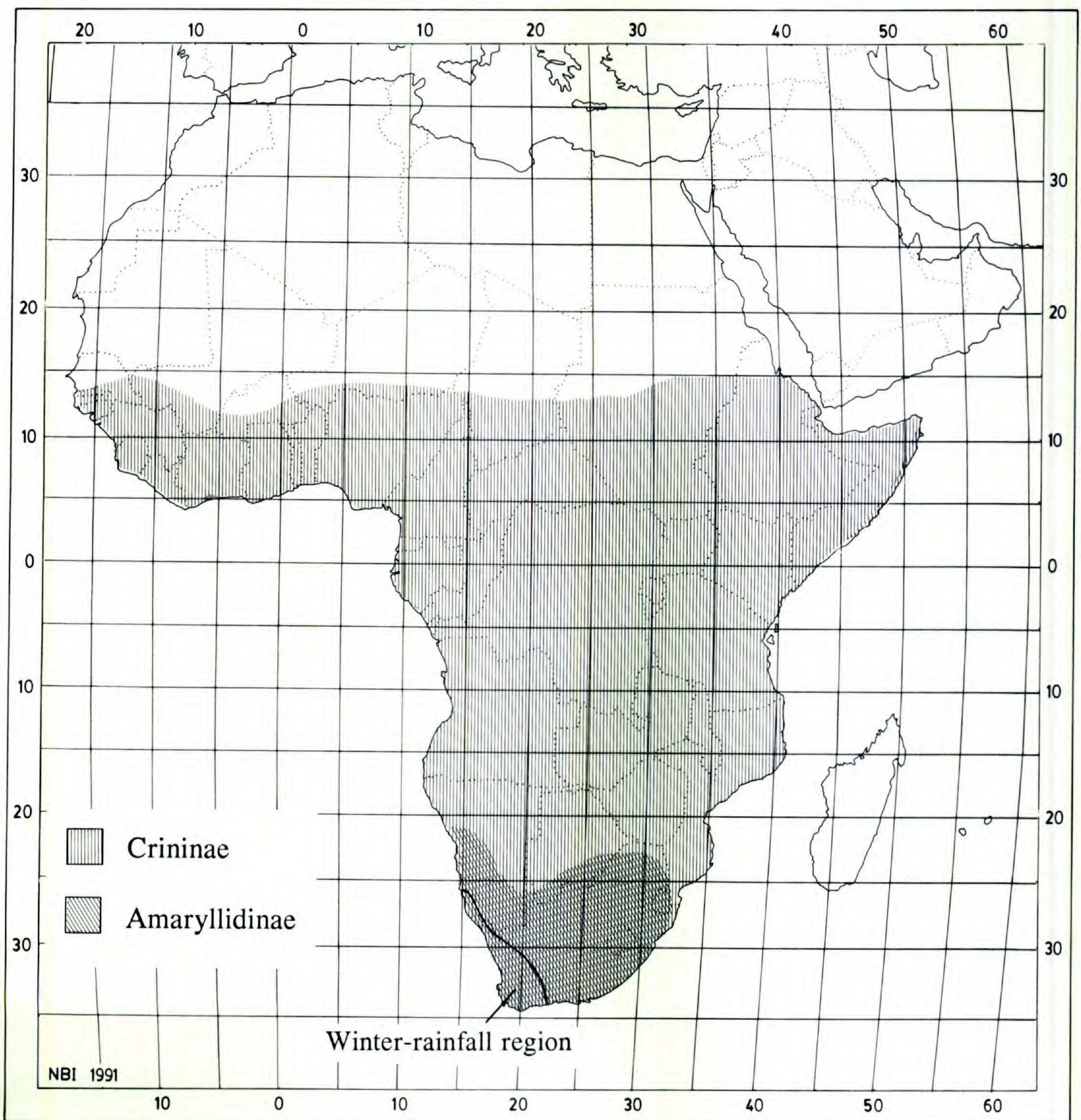
Figure 3.   Distributions of subtribes Amaryllidinae and Crininae in Africa.

commented on by several authors (see Rendle, 1901), the seeds are large (at most 20–30 mm across in *Crinum*) but not necessarily heavy (Boyd, 1932; Dutt, 1962), and they germinate easily without additional water (Beaurieux, 1914; Howell & Prakash, 1990; Isaac & McGillivray, 1965). In comparison to other Amaryllidaceae, the embryos of Amaryllideae seeds have a cotyledon with a particularly well-developed vascular system that contributes to seedling vigor, as reported by Boyd (1932). This can be seen in the rapid elongation of the hypogeal cotyledon, which assists the primary root to bore deeply into the soil and allows bulb

formation within the first two months after germination (Clark & Parsons, 1994, pers. obs.).

Embryological studies (Dutt, 1962; Schlimbach, 1924; Venkateswarlu & Lakshmi, 1978) have shown that the mass attained by Amaryllideae seeds is due either to the development of the ovule's solitary integument or to the endosperm. Consisting of up to 25 cell layers, the single integument in Amaryllidinae (except *Amaryllis*) is well developed relative to the endosperm (Fig. 4B). As first reported by Schlimbach (1924), stomata are present in the testa (Fig. 4D), and the integument has considerable amounts of chlorophyll and starch (Fig.
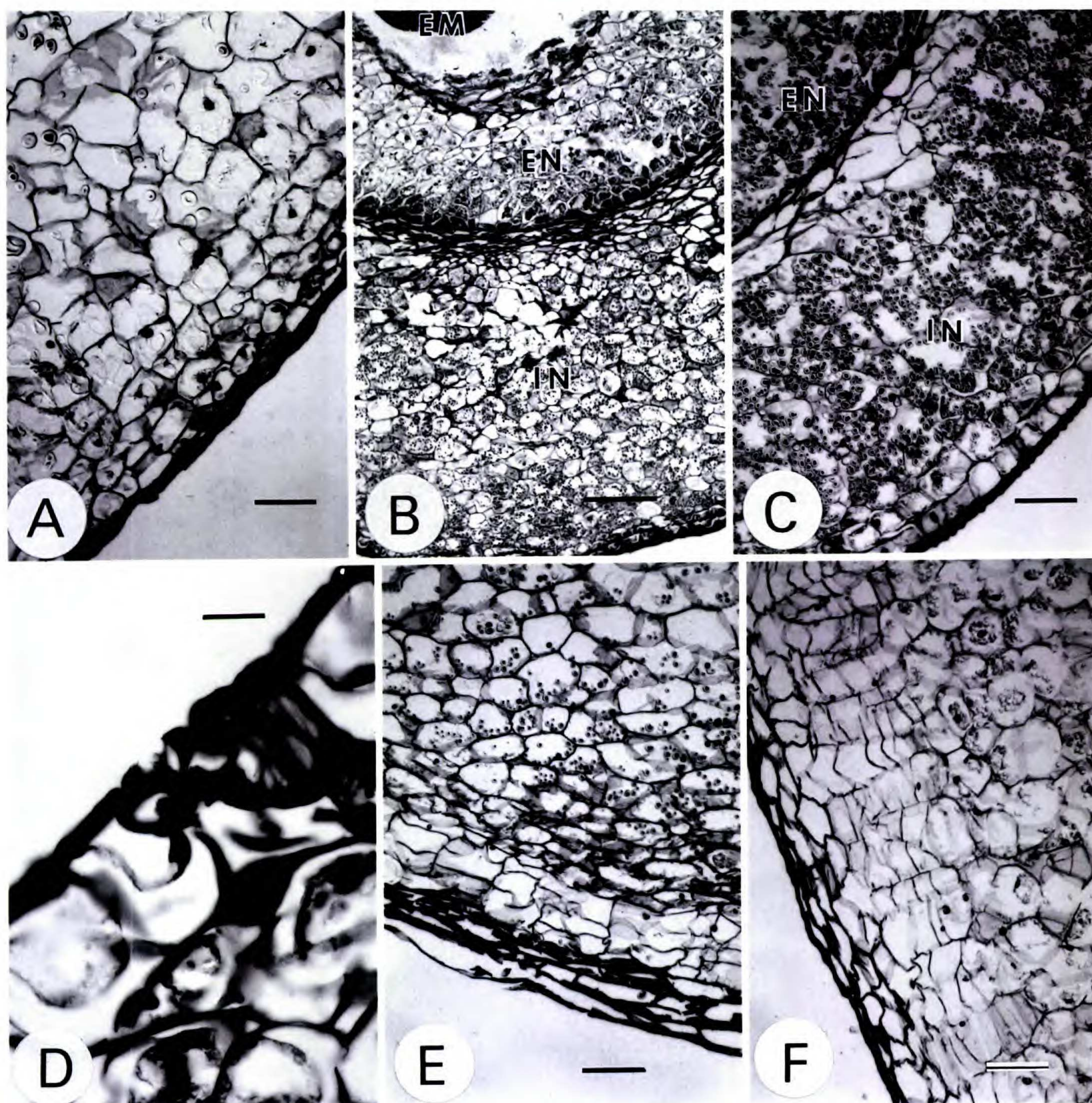
Figure 4. Seed anatomy in Amaryllideae. A–D. Species in subtribe Amaryllidinae.—A. *Amaryllis belladonna*; note the cells of the endosperm containing plastids and the partially disintegrated integument forming the testa.—B. *Brunsvigia josephinae*; part of the embryo, endosperm, and well-developed integument.—C. *Brunsvigia radula*; part of the endosperm and integument densely packed with starch grains.—D. *Strumaria chaplinii*; outer layers of integument showing chloroplasts and a stoma in cross section. E, F. Species in subtribe Crininae.—E. *Cybistetes longifolia (Duncan 81)*; endosperm showing mature cork and phellogen surrounding the inner layers of starch-filled cells.—F. *Ammocharis coranica*; endosperm with phellogen and cork in the outer layers; note chloroplasts and starch grains in the inner cells. Scale bars: A, C, E, F = 100 μm; B = 250 μm; D = 25 μm. EM = embryo, EN = endosperm, IN = integument. Appendix I gives details of voucher specimens.

4B, C). The stomata are anomocytic (Fig. 5B–E) and the suprastomatal cavity is overarched by lobes of the adjacent epidermal cells. The epidermis is covered by a thick, sculptured cuticle (Fig. 5D, E) in which the striations become increasingly sinuous with age. Growth of the embryo is delayed during the development of the accessory seed tissues (Goebel, 1932; Schlimbach, 1924), and the embryo remains small relative to that of Crininae when the

seed is shed. *Amaryllis*, with its large, irregular, white to pink seeds, is exceptional in the tribe in that it has chlorophyll only in the embryo. The seed of *Amaryllis* possesses mainly endosperm (Hofmeister, 1861), without noticeably large amounts of starch (Fig. 4A), and the integument provides only the testa (Schlimbach, 1924), which lacks stomata (Fig. 5A).

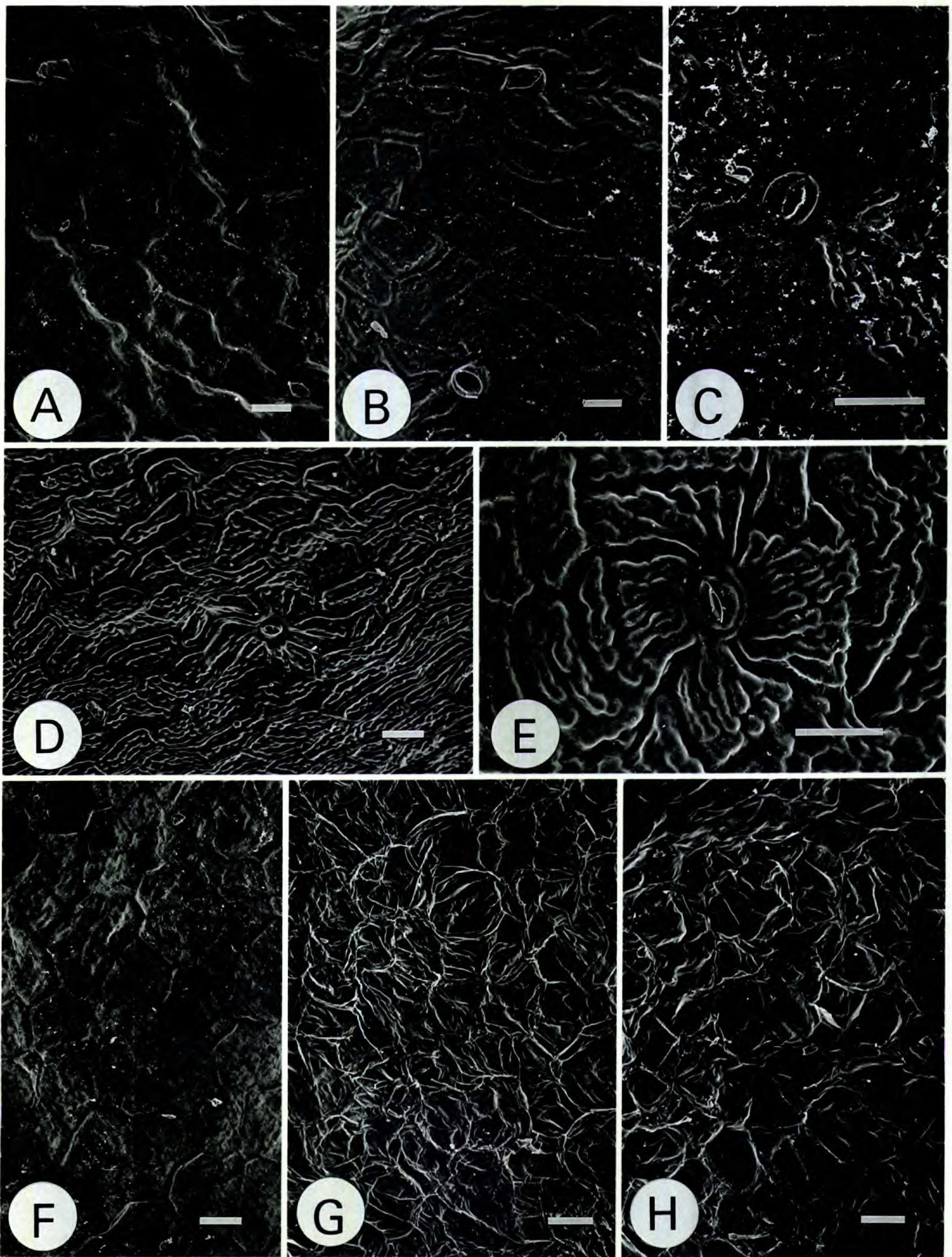In contrast, the solitary integument and nucellus

Figure 5.   Seed surfaces in Amaryllideae. A–E. Species in subtribe Amaryllidinae; note the presence of stomata except in *Amaryllis.*—A. *Amaryllis belladonna.*—B. *Brunsvigia orientalis.*—C. *Nerine filifolia.*—D. *Strumaria truncata.*—E. *Hessea breviflora*, showing detail of the thick sinuous cuticle. F–H. Species in subtribe Crininae; note the corky surface at different stages of maturity.—F. *Boophone disticha.*—G. *Crinum variabile.*—H. *Ammocharis coranica.* Scale bars: 50 μm. See Appendix I for details of voucher specimens.

of Crininae are transitory and absent from the fully developed seed (Dutt, 1962, 1970). The mature seed consists of massive amounts of starch-containing endosperm. The endosperm is differentiated into cork in the outermost layers (Fig. 5F–H) and has several layers of chlorophyll-containing cells immediately below the phellogen (Fig. 4E, F). The seeds of Crininae are larger (10–30 mm diam.), more irregular and angular than the ovoidal, stomatose seeds (4–10 mm diam.) of the Amaryllidinae. The embryo is well developed when the seed is shed, and the orientation of the embryo with respect to the seed as a whole is arbitrary (Toilliez-Genoud, 1965). Cotyledon extension is positively geotropic even within the seed (Howell & Prakash, 1990).

The chlorophyllous tissue present in the integument of the *Nerine–Brunsvigia–Crossyne–Hessea–Carpolyza–Strumaria* clade and in the outer layers of the endosperm in Crininae implies some functional activity. Tests with infrared gas analysis showed that seeds of representatives from both subtribes (*Brunsvigia orientalis* (L.) Eckl. & Zeyh. and *Cybistetes longifolia* (L.) Milne-Redh. & Schweick.) are photosynthetically active and that those with a well-developed integument are capable of photosynthesis at lower light levels than those of Crininae (Wand, pers. comm.). Furthermore, a test for durability in water indicated that seeds of *C. defixum* Ker Gawl. and *C. flaccidum* Herbert had unimpaired germination when removed from fresh water after four months (Clark & Parsons, 1994; Dutt, 1962), although fresh water increases susceptibility to pathogen invasion (Manasse, 1990), and when wounded, the damaged outer portions of *Crinum* seeds rapidly produce fresh cork tissue (Dutt, 1962; Merry, 1937). Tests on the buoyancy and viability of *Crinum* seeds in salt water indicate that they can float and remain viable for more than two years (Koshimizu, 1930).

The phylogeny generated by the morphological data reveals little about the character assembly of the three seed types that exist in Amaryllideae. All the seed characters for Crininae (characters 31 and 32, Fig. 2) appear at the same branch point of the phylogeny; similarly, the seed characters for *Nerine, Brunsvigia, Crossyne, Hessea, Carpolyza,* and *Strumaria* resolve at a single node (characters 28, 29, and 30, Fig. 2). In general, this pattern suggests that the selective association between these characters is strong (Armbruster, 1992; Frumhoff & Reeve, 1994), but, in the absence of additional data, our interpretation remains tentative. Relative to the bitegmic ovule and dry seeds of the outgroup, it is evident that the unitegmic ovule and fleshy

seeds of Amaryllideae arose at the base of the lineage, through the loss of an integument in the ovule and the loss of the metabolic activity that leads to maturation drying in the seed. The solitary integument persisted and thickened in the seeds of the Amaryllidinae lineage, and chlorophyll and stomata developed. In Crininae, the integument became short-lived and disappeared from the seed, but abundant endosperm and a corky covering were developed. Thus, apart from a major divergence in seed morphology subsequent to the origin of the fleshy, nondormant seed in Amaryllideae, no prevailing sequences in the origin of the different seed characters are evident.

EVOLUTION OF DISPERSAL SYSTEMS IN AMARYLLIDEAE

Wind dispersal (anemochory) occurs in six genera of Amaryllideae (Fig. 6), and in all but one of these clades the mode of wind dispersal is anemogeochorous (sensu Van der Pijl, 1982). The functionally interrelated characters shared by the five anemogeochorous taxa are low stature, lightness of the infructescence; detachment of the infructescence as a single unit before seed release (characters 22(2) and 23, Fig. 2); and long, stiff pedicels (character 9, Fig. 2) that radiate outward in all directions. Despite the similarities in the morphology and manner in which the infructescences of each genus are blown over the ground, subtle differences are evident in the dispersal units' structure and tumbling, skidding, or lofting ability.

Particularly good tumblers have been observed among representatives of the *Brunsvigia–Crossyne* clade. In many *Brunsvigia* species this ability appears to be associated with broad, kitelike capsule surfaces (Fig. 7A, B), a characteristic that is recognized to be optimal for ease of rolling (Maddox & Carlquist, 1985; Van der Pijl, 1982). This specialization is further enhanced by the tardy dehiscence of the capsules, which prolongs the period over which seed is scattered. In *Crossyne* the infructescences are uniformly spherical due to the exceptionally large number of pedicels (100 or more), and these equal the scape in length (Fig. 7C). When released, contact with the ground is minimal and little force is required to roll the balllike infructescence.

Relative to other representatives of Amaryllideae, *Hessea, Carpolyza,* and *Strumaria* are characteristically diminutive in size. The narrowly distributed, wind-dispersed species of *Hessea* and *Strumaria* subg. *Gemmaria* have infructescences in which the pedicels often remain shorter than the scape (ca. half the length of the scape) and are few
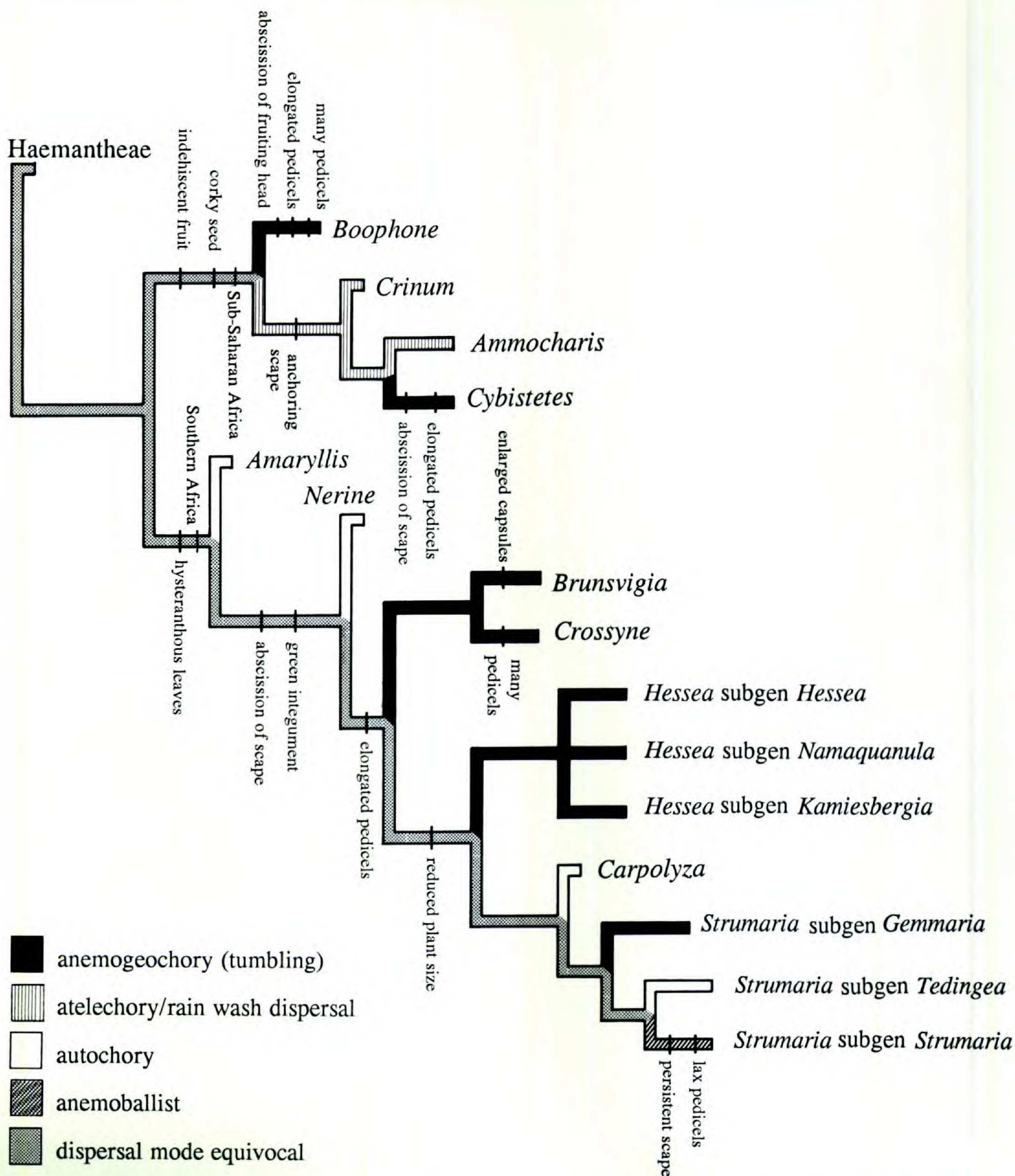
Figure 6. Dispersal systems, plant phenology, phytogeography, and functionally related seed and fruit characters in Amaryllideae mapped onto the cladogram given in Figure 2.

in number. Although this configuration has some wind dispersal ability, it appears to be optimal for lodging in rock crevices and damp depressions, and in some species (*H. monticola* Snijman, *H. cinnamomea* (L'Hérit.) Durand & Schinz, and *H. mathewsii* W. F. Barker) the infructescences have been observed to interlock so that the seeds are locally concentrated (Fig. 7D).

In *Boophone* sensu stricto the more or less spherical shape of the infructescence is attained by the

rapid elongation of the large number of pedicels after anthesis (Fig. 7G). Thereafter (ca. six weeks), the dried fruiting head breaks away from the top of the scape (character 23, Fig. 2) and is lofted or blown horizontally by the wind. Since the scape remains attached to the bulb, the cohesiveness of the released fruiting head is weakened and it may break into subunits before lodging. The seeds, held by the indehiscent dry fruits, are gradually released as the papery walls disintegrate during transport.
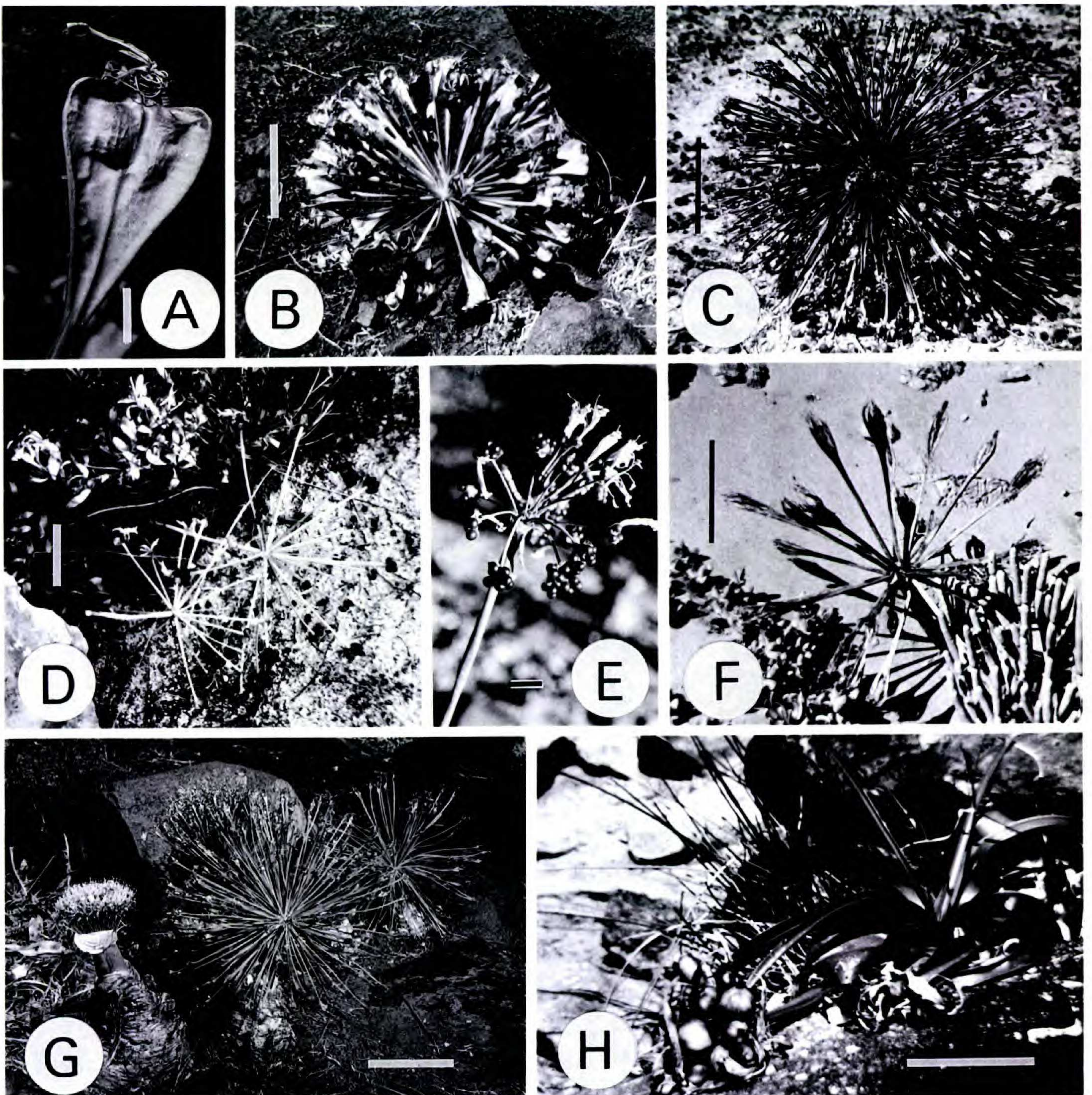
Figure 7.   Infructescences of various South African winter-rainfall species of Amaryllideae.—A, B. *Brunsvigia bosmaniae*; detail of kitelike capsule, wind-blown infructescence.—C. *Crossyne flava*; intact infructescence showing the numerous, symmetrically arranged pedicels.—D. *Hessea monticola*; detached, interlocked infructescences each with few pedicels.—E. *Strumaria truncata*; note the lax, pendulous pedicels.—F. *Cybistetes longifolia*; a wind-rolled infructescence showing frayed, worn-down fruits.—G. *Boophone haemanthoides*; note the elongation of the pedicels after flowering.—H. *Crinum variabile*; showing the mature fruits dropped close to the parent plant. Scale bars: A, E = 1 cm; B–D, F–H = 10 cm.

The infructescence configuration of *Cybistetes* is essentially similar to that of many *Brunsvigia* species; however, the indehiscent, protective, strongly ribbed, dry fruits are dependent on being worn down by rolling (Fig. 7F), a process that gradually releases the seeds.

From the character distribution, the secondary loss of the abscission zone in the scape, and a reversal to short, lax pedicels (characters 9 and 22(0), Fig. 2) have apparently given rise to one further method of wind dispersal in representatives of *Stru-*

maria subg. *Strumaria*. In this group the fruiting head does not detach and the seeds are individually released relatively high above the ground surface. The pedicels in *S. truncata* Jacq., *S. barbarae* Oberm., and *S. hardyana* D. & U. Müll.-Doblies are flexible and pendulous and swing to and fro in strong winds so that seeds are widely scattered from the parent plant (Fig. 7E). Unlike the secondary transportation of the seed in other wind-dispersed Amaryllideae, the trajectory of the seed in *Strumaria* subg. *Strumaria* is direct from plant to

ground, and belongs to the dispersal class of ane-moballists (Van der Pijl, 1982).

The sequence of character assembly in the phylogeny suggests that the development of anemogeochory in Amaryllidinae possibly commenced with the hysteranthous leaf habit, which is almost basal to the subtribe (Fig. 6), followed by the development of an abscission layer in the scape at ground level and thereafter by an inflorescence with long pedicels (Fig. 6). In combination, these characters appear to have resulted in the shedding of the infructescence at a time when the effect of the vegetative cover as a potential windbreak was minimal, and with a configuration that could have supported the transition of the entire infructescence into a single, complex unit, in which other characters associated with wind dispersal could be independently derived. These further specializations (Fig. 6) mostly reflect small quantitative changes: increased capsule surface (Brunsvigia), increased pedicel number (Crossyne), and altered pedicel length (Brunsvigia, Crossyne, Hessea, and Strumaria).

In contrast, neither hysteranthous leaves nor an abscission zone in the scape are basal to subtribe Crininae. The apparent absence of an historical transition toward the light, spherical, detaching infructescences of Boophone and Cybistetes (Fig. 6) suggests that the assembly of characters suited to anemogeochory in these two lineages was extremely rapid, or that the intermediate ancestral species are extinct. The differences in the situation of the abscission zone in the scape of Boophone sensu stricto and Cybistetes (at the top of the scape and at ground level, respectively) imply that the dispersal units of these genera are independently derived structures. This indicates that anemogeochory evolved twice in Crininae. The interpretation for Amaryllidinae, however, remains ambiguous. Two equally parsimonious hypotheses can be proposed. Either anemogeochory evolved independently in three lineages of Amaryllidinae (in the Brunsvigia–Crossyne clade, the Hessea clade, and in Strumaria subg. Gemmaria); or anemogeochory evolved only once in the Brunsvigia–Strumaria clade and was subsequently lost in Carpolyza and in the Strumaria clade consisting of subgenera Strumaria and Tedingea. Either interpretation, however, suggests that the fruiting characters associated with wind dispersal are plastic.

Dispersal by tumbling is restricted to and consistently present in the five genera and one subgenus of Strumaria that we have discussed. With the exception of only Boophone, all are confined to southern Africa and, with the exception of some

Brunsvigia and Strumaria species, all are concentrated in the western half of South Africa. The highest concentrations of Amaryllideae species with the anemogeochorous habit (based on the number of species recorded in BOL, NBG, PRE, and SAM per 15' × 15' grid area) are in the west of the Northern Cape (grid 3119AC, eight species), Namaqualand (grids 2917BA, 3017BB, 3118DA, and 3118DB, five species each), and the Western Cape (3319CB, six species; 3420BC, five species). This clearly indicates that wind dispersal in Amaryllideae is more common in South Africa than in the rest of Africa and that the semiarid, winter-rainfall region has the greatest diversity of wind-dispersed representatives.

Ellner and Shmida (1981) found similarly high concentrations of taxa adapted to tumbling in the semi-desert areas of Israel, and Maddox and Carlquist (1985) reported wind dispersal in many Californian desert plants. Van der Pijl (1982) stressed the association between wind dispersal and biotic poverty, particularly in pioneer vegetation, whereas the studies of Maddox and Carlquist (1985) concentrated on the importance of wind in determining the dispersal mode of desert plants. The winter-rainfall region of southern Africa encompasses two biomes (Rutherford & Westfall, 1986) in which wind and disturbance are major features. The Fynbos Biome offers numerous transient niches through frequent fire (Cowling, 1987) and the Succulent Karoo Biome, with a 15–50% canopy cover (Hilton-Taylor, 1994), offers many more persistently open sites. Wind in both biomes is reported to exceed that of similar climatic regions elsewhere in the world (Deacon et al., 1992).

The other major dispersal specialization in Amaryllideae is represented in the Crinum–Ammocharis clade (Fig. 6), where the seeds are large, the fruits are variable, and the infructescences have no wind dispersal ability. Most species of Crinum and Ammocharis have green and membranous to brown and papery fruits; however, the fruit walls of a few tropical species of Crinum (C. delagoense I. Verd., C. kirkii, Baker, C. papillosum Nordal, and C. stuhlmanii Baker) are berrylike with a red to orange, thick or spongy pericarp (Nordal, 1982). This trend corresponds with Dahlgren and Rasmussen's (1983) hypothesis that baccate fruits in Amaryllidaceae are secondarily derived. The somewhat lax scapes and short pedicels of these genera, whose representatives commonly occupy washes, salt pans, or streambeds (Table 3), do not detach from the bulb. After anthesis the scape elongates, bends downward, and either rests on the ground (Fig. 7H) or droops into water. Until the walls grad-

ually disintegrate, the seeds are retained in the indehiscent fruit close to the parent plant. Depending on local conditions, the angular seeds germinate where they were deposited or their buoyancy allows them to be carried into seasonal washes and stream beds or the floodplains of permanently flowing rivers (Clark & Parsons, 1994; Manasse, 1990, pers. obs.).

Limited dispersal has been regarded either as a strategy to recapture a favorable site where suitable habitats are limited (Zohary, 1962) or alternatively as a product of specialized seed-containers which serve primarily to protect and regulate the timing of dispersal and germination (Ellner & Shmida, 1981). The loss of an opening mechanism in the fruit at the base of the Crininae lineage (character 24, Fig. 2) and the development of a large seed with a specialized endosperm at the same point of the phylogeny (characters 31 and 32, Fig. 2) suggest an early evolutionary association between the indehiscent fruit and the large seeds in Crininae. The subsequent development of the anchoring function by the persistent, lax scape in *Crinum* and *Ammocharis* (Fig. 6) suggests, therefore, that temporal limitation preceded spatial limitation of seed dispersal in Crininae. A critical analysis of the evolutionary sequence of dispersal and protective functions nevertheless awaits tests on the role that the berrylike fruits of *Crinum* may play in protecting the developing seeds from possible microbial damage in moist subtropical or tropical terrestrial habitats (see Corner, 1992).

The presence of both wind- and water-dispersal mechanisms in Crininae indicates greater diversity in dispersal mode in Crininae than in Amaryllidinae. Since particularly large, endosperm-rich seeds are basal to the Crininae lineage, this pattern supports the hypothesis (Stebbins, 1970) that taxa having large seeds are particularly subject to selection pressures favoring special mechanisms for seed dispersal. Although Clark and Parsons (1994) suggested that ravens may carry and drop seeds of *Crinum flaccidum*, biotic dispersal of the fleshy seeds has never been recorded in the tribe. The large, water-rich seeds of Amaryllideae, which are borne near the ground and dropped at or near maturity, have no smell (pers. obs.). Except in *Amaryllis*, the seeds lack attractive coloring and none require burial for germination (Isaac & McGillivray, 1965; Rendle, 1901, pers. obs.). These characteristics match none of the syndromes that Van der Pijl (1982) has identified as adaptive for biotic dispersal. It seems possible that the highly toxic alkaloids, which are widely present in the tribe (see Watt & Breyer-Brandwijk, 1962), may have limited seed

predation (see Manasse, 1990) and the development of seed and fruit specializations primarily associated with reptile, bird, or mammalian dispersal agents, and conversely, may have promoted the tribe's evolutionary development toward the exploitation of diverse abiotic dispersal mechanisms.

EVOLUTIONARY PATTERNS IN THE ECOLOGY OF AMARYLLIDAEAE

It is well accepted that new periods of evolutionary vigor and new diversification coincide with the conquest of new biological niches, by means of new features (Riedl, 1978). Characters that permit a fairly rapid departure of a group of organisms from a preceding ecological sphere are referred to as key innovations by Larson et al. (1981). Moreover, such innovations are considered to promote the appearance of supportive adaptations during the ecological transition.

The developmental stage at which selective pressures would be expected to be maximal is that of early seedling development (Stebbins, 1974). Thus for Amaryllideae we suggest that seedling vigor, associated with the green embryo of the large nondormant seed, probably contributed to the widespread radiation of many ancestral species of the group throughout sub-Saharan Africa during the early Tertiary when seasonally moist subtropical/tropical conditions prevailed (see Axelrod & Raven, 1978). With the subsequent aridification of Africa and the inception of extreme summer-aridity in southwestern Africa during the Pliocene (Deacon et al., 1992; Tankard & Rogers, 1978), a postulated key innovation for Amaryllidinae was the development of a seed with a large, green integument and stomatose testa. Since the integument is thought to enable the seed to photosynthesize and ripen independently of the parent plant (Goebel, 1932), this novel feature of post-ripening is considered to have facilitated the accelerated shedding of the infructescence, and so promoted the transition of the entire infructescence into a unit, highly specialized for wind dispersal (Fig. 6). This occurred especially in the semiarid, winter-rainfall region of southwestern Africa where the short growing season favored the seed's rapid release to coincide with the onset of the rainfall season, and the extreme winds favored the development of anemogeochory.

With increasing aridity the phylogenetic hypothesis for Crininae reflects a different evolutionary strategy. The subtribe's present distribution suggests that the evolution of its large seed was mainly promoted in the summer-rainfall regions of sub-Saharan Africa, where the duration of the growing

season imposed little limitation on seed size. *Boophone* and *Cybistetes* adapted to dry, open sites, but many species of *Crinum* and *Ammocharis* adopted a hydrophilic habit that allowed them to survive at the margins of permanent and seasonal water bodies. A key innovation that possibly permitted Crininae to evolve both xerophilic and hydrophilic habits was the development of a protective, ecologically versatile, corky seed covering, whose water-resistant and insulating qualities led to the evolution of wind- and water-dispersal mechanisms (Fig. 6) during the climatic changes of the Pliocene. The occurrence, however, of only three wind-dispersed Crininae species in the winter-rainfall of south-western Africa area may reflect an intrinsic constraint to the production and timely release of the lineage's large seeds in a region where the growing season is short. Furthermore, although the pantropical distribution of *Crinum* may reflect a former Gondwanan distribution, the development of water dispersal and the tolerance of *Crinum* seeds for saline conditions supports Koshimizu's (1930) and Arroyo and Cutler's (1984) suggestion that long-distance dispersal events may have been influential in the past. We propose that the concentration of a great number of *Crinum* species in southern Africa (Nordal, 1977; Verdoorn, 1973) is a consequence of its atelechorous/rain wash dispersal mechanism which, together with the inability to develop stored seed banks, resulted in high rates of isolation, migration, and extinction among the ancestral taxa inhabiting the seasonal water systems in the increasingly arid regions of the west.

CONCLUSION

Character distribution in the Amaryllideae indicates constancy in floral and vegetative morphology relative to the diversity shown in the seed and fruiting structures. Seed characters have been shown to have greatest diagnostic value at the tribal and subtribal level. A single integument, at least at some stage of the seed's development, and a green embryo are synapomorphic for the tribe. Large cork-covered, green, endosperm-rich seeds characterize Crininae, and seeds with a green, stomatose integument are characteristic of all Amaryllidinae other than *Amaryllis*. Elsewhere in Amaryllidaceae, fleshy seeds also occur in the African tribe Haemantheae and the mainly American tribe Eucharideae, but so far little is known about their phylogenetic importance or ecology (Meerow, 1989). In contrast, the phylogeny of Amaryllideae, combined with data on dispersal, germination, and distribution patterns, suggests that much of the diversifi-

cation in Amaryllideae arises from the group's novel seed characters. We propose that the specialized seed morphology and the unique and complex dispersal systems in Amaryllideae reflect a series of altered compromises that developed during the climatic changes of the past; in particular between the selection pressures that favored large, nondormant seeds, and those that favored diverse but efficient modes of seed dispersal. The seed-dispersal mechanisms that have evolved in Amaryllideae are all associated with abiotic agents, predominantly wind and water, whereas biotic dispersal remains unknown in the tribe.

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Appendix I. Amaryllideae material examined for seed micromorphology. Vouchers marked with an asterisk were also used for infrared gas analysis.

Amaryllis belladonna L., South Africa, Vredenburg, *Snijman 848* (NBG); *Ammocharis coranica* (Ker Gawl.) Herb., South Africa, Bloemfontein, *Müller 415* (NBG).

Boophone disticha (L.f.) Herb., South Africa, Montagu, *Snijman 1268* (NBG); *Boophone haemanthoides* F. M. Leight., South Africa, Nieuwoudtville, *Snijman 588* (NBG); *Brunsvigia bosmaniae* F. M. Leight., South Africa, Karkams, *Snijman 275* (NBG); *Brunsvigia comptonii* W. F. Barker, South Africa, Laingsburg, *Snijman s.n.* (NBG 151858); *Brunsvigia josephinae* (Redouté) Ker Gawl., South Africa, Worcester, *Compton 20484* (NBG); *Brunsvigia litoralis* R. A. Dyer, South Africa, Jeffreys Bay, *Malan 137* (NBG); *Brunsvigia minor* Lindl., South Africa, farm Arendskraal, *Snijman 596* (NBG); **Brunsvigia orientalis* (L.) Eckl. & Zeyh., South Africa, near Vanrhynsdorp,

Snijman 437 (NBG); *Brunsvigia radula* (Jacq.) W. T. Aiton, South Africa, Knersvlakte, *Snijman 1254* (NBG).

Crinum variabile (Jacq.) Herb., South Africa, Bowesdorp, *le Roux s.n.* (NBG 892/82); *Crossyne guttata* (L.) D. & U. Müll.-Doblies, South Africa, Montagu, *Snijman 1259* (NBG); *Crossyne flava* (W. F. Barker ex Snijman) D. & U. Müll.-Doblies, South Africa, Grootvlei, *Perry 1126* (NBG); **Cybistetes longifolia* (L.) Milne-Redh. & Schweick., South Africa, Beauvallon, *Williamson 4637* (NBG); *Cybistetes longifolia* (L.) Milne-Redh. & Schweick., South Africa, Gordon's Bay, *Duncan 81* (NBG).

Hessea breviflora Herb., South Africa, Arabies, *Williamson 3431* (NBG); *Hessea mathewsii* W. F. Barker, South Africa, farm Skaapplaas, *Snijman 842* (NBG); *Hessea pusilla* Snijman, South Africa, farm Perdekraal, *Snijman 1072* (NBG); *Hessea stenosiphon* (Snijman) D. & U. Müll.-Doblies, South Africa, Kamiesberg, *Snijman 1179* (NBG).

Nerine bowdenii W. Watson, South Africa, Harrismith, *Schelpe s.n.* (NBG 878/75); *Nerine filamentosa* W. F. Barker, South Africa, Cathcart, *MacMaster s.n.* (NBG 148/85); *Nerine filifolia* Baker, South Africa, Harrismith, *Schelpe s.n.* (NBG 877/75); *Nerine marincowitzii* Snijman, South Africa, SE of Leeu-Gamka, *Snijman 1245* (NBG); *Nerine masonorum* L. Bolus, South Africa, near Mquanduli, *Cannon & Mason s.n.* (NBG 66355); *Nerine undulata* (L.) Herbert., South Africa, Engcobo, *Gibson s.n.* (NBG 59983).

Strumaria aestivalis Snijman, South Africa, Langberg, *Perry 1991* (NBG); *Strumaria chaplinii* (W. F. Barker) Snijman, South Africa, Paternoster, *Barker 10239* (NBG); *Strumaria gemmata* Ker Gawl., South Africa, Baviaanskloof, *Vlok 956* (NBG); *Strumaria karooica* (W. F. Barker) Snijman, South Africa, Sutherland, *Forrester & Leitch s.n.* (NBG 145851); *Strumaria karoopoortensis* (D. & U. Müll.-Doblies) Snijman, South Africa, Fonteinskop, *Perry 1278* (NBG); *Strumaria pygmaea* Snijman, South Africa, farm Kersbosvlei, *Snijman 862* (NBG); *Strumaria tenella* (L.f.) Snijman subsp. *orientalis* Snijman, South Africa, Bloemfontein, *Oliver 313* (NBG); *Strumaria truncata* Jacq., South Africa, Steinkopf, *Perry 1057* (NBG).